

Interactions of onion (*Allium cepa*) and yellow wax bean (*Phaseolus vulgaris*) in monoculture and intercropping with weeds, *Chenopodium album* and *Amaranthus hybridus*

by

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Abstract

Intercropping systems are seen as advantageous as they can provide higher crop yield and diversity along with fewer issues related to pests and weeds than monocultures. However, plant interactions in intercropped crop species and between crops and weeds in these systems are still not well understood. The main objective of this study was to investigate interactions between onion (*Allium cepa*) and yellow wax bean (*Phaseolus vulgaris*) in monocultures and intercropping with and without the presence of a weed species, either *Chenopodium album* or *Amaranthus hybridus*. Another objective of this study was to compare morphological traits of *C. album* from two different populations (conventional vs. organic farms). Using a factorial randomized block design, both crop species were planted either in monoculture or intercropped with or without the presence of one of the two weeds. The results showed that intercropping onion with yellow wax bean increased the growth of onion but decreased the growth of yellow wax bean when compared to monocultures. The relative yield total (RYT) value was 1.3. Individual aboveground dry weight of both weed species under intercropping was reduced about 5 times when compared to the control. The poor growth of weeds in intercropping might suggest that crop diversification can help resist weed infestations. A common garden experiment indicated that *C. album* plants from the conventional farm had larger leaf area and were taller than those from the organic farm. This might be associated with specific evolutionary adaptation of weeds to different farming practices. These findings contribute to the fundamental knowledge of crop-crop interactions, crop-weed competition and adaptation of weeds to various conditions. They provide insights for the management of diversified cropping systems and integrated weed management as practices in sustainable agriculture.

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I dedicate this thesis to my grandparents. I didn't get to tell you that I love you but I always do. I know that you are watching over upon me with love and protection. Thank you for everything. We miss you. - Love, your grandson

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Introduction

The concept of sustainable agriculture attempts to integrate three major goals: environmental safety, economic profitability and social equity (Malézieux *et al.*, 2009). Concerns of sustainable agriculture highlight the need for practices that can ensure crop productivity and at the same time, reduce damage to the environment (Lithourgidis *et al.*, 2011). Modern agriculture is dominated by intensive monocultures, which causes the loss of biodiversity and ecological functions (Malézieux *et al.*, 2009). Biodiversity of an ecosystem maintains ecological services such as nutrient cycling, tolerance to pest occurrences and disease outbreaks (Malézieux *et al.*, 2009; Steudel *et al.*, 2012). Low crop diversity in monoculture results in its susceptibility to environmental stresses and high reliance of external inputs and management to control pests and weeds (Lin, 2011; Steudel *et al.*, 2012). Agricultural diversification contains agricultural practices that use ecological principles to increase the productivity and stability of agroecosystems (Lin, 2011; Tilman *et al.*, 2012). A growing number of studies on agricultural diversification such as agroforestry and intercropping (i.e. use of two or more crop species simultaneously) have been promoted as types of sustainable agriculture (Lithourgidis *et al.*, 2011).

Intercropping, for example, has multiple advantages such as potential to increase total yield, improve soil fertility and reduce insect pest and weed incidences without the use of agrochemicals that can be harmful to the environment (Malézieux *et al.*, 2009; Lithourgidis *et al.*, 2011). However, the mixture of crop species in intercropping systems leads to complex plant species interactions (e.g. competition and facilitation). These interactions can have direct or indirect effects on the growth and productivity of the crops

(Sobkowicz and Podgórska-Lesiak, 2007; Malézieux *et al.*, 2009). A better understanding of plant-plant interactions between the mixture of species and the proper management of these interactions is the main concern in designing and managing a diversified cropping system (Sobkowicz and Podgórska-Lesiak, 2007).

Interactions among plant species in natural environments are important processes affecting plant community composition and productivity (Keddy, 1989). In agricultural ecosystems, studies on crop-crop and crop-weed interactions, even though originally aimed at improving the yield of agricultural crops, have recently been used to investigate more basic ecological questions (Bracken, 2008; Aspasia *et al.*, 2009; Malézieux *et al.*, 2009). Comparing performance of plant species in monocultures vs. polycultures is a way to understand interaction mechanisms among plant species (Bracken, 2008). Experiments on plant growth, fecundity, resource allocation, and morphological and physiological responses in monocultures vs. polycultures are used to evaluate the degree of intra- and inter-specific competition and facilitation among plants (Bracken, 2008). In addition, since the mixture of crop species is linked to ecological questions about the relationship between species diversity and ecological functions, comparisons between monocultures and polycultures have been used in studies of invasion ecology, including the importance of crop diversification and reduction of weeds or pest invasions (Fargione and Tilman, 2005; Bracken, 2008).

Weeds represent a group of plant species that impact crop production. They have high competitive ability and great tolerance to intensive disturbances (Murphy and Lemerle, 2006). However, the success of weed invasions not only depends on their competitive traits but also relates to the invasion potential (invasibility) of an ecosystem

(Milbau *et al.*, 2005). This suggests that the competitive ability of crop species and the degree of efficiency of resource use in agroecosystems can affect the success of weed invasions (Fargione and Tilman, 2005). Moreover, in the long term, weeds may experience generation after generation competition against a single crop species (depending on the crop rotation schedule) or other repeated agronomic practices such as the use of herbicides, fertilizers or mechanical weeding, resulting in rapid adaptation to these local conditions and gradually leading to evolutionary responses to these selective pressures (Weinig, 2005 Murphy and Lemerle, 2006). These evolutionary responses in weeds may lead to the reconsideration of current weed management and the innovation of further weed control methods (Bommarco *et al.*, 2010).

Current understanding of plant interactions in monocultures vs. polycultures and the evolutionary consequences of weed selection by cultivation practices are only partially understood. Studies on these issues can not only contribute to the development of more profitable and environmentally friendly cultivation practices but also provide better understanding to the basic ecological and evolutionary mechanisms of plant interactions and plant invasions. In the following sections, current ecological knowledge in plant-plant interactions under monoculture vs. polyculture systems and the evolutionary adaptation of agricultural weeds to different agronomic practices will be reviewed.

1. Plant-plant interactions in agroecosystems

1.1. *Intraspecific competition*

In conventional monocultures where herbicides are largely used to exclude weeds, the major plant interaction is intraspecific competition (competition among individuals of the same species). Intraspecific competition is considered to be intensive since individuals of the same species have the same requirements for space and resources (Keddy, 1989). Three main effects caused by intraspecific competition in monocultures due to density dependence are: competition-density effect (decrease in mean plant biomass with increasing density), size inequality (alteration of size structure at high density) and self-thinning (increase in mortality at high density) (Kira *et al.*, 1953; Yoda *et al.*, 1963; Fibich *et al.*, 2014). In agronomic environments, planting densities barely reach the level where self-thinning would be expected to occur (Park *et al.*, 2003). But competition-density and size inequality effect have been described in many population models of monocultures (Park *et al.*, 2003). For example, increasing planting density of onion (*Allium cepa* L.) causes reduction in individual plant biomass, decrease in the number of large bulbs and increase in the production of small sized bulbs due to intensive competition for space and soil nutrients (Kahsay *et al.*, 2014). Farmers increase crop planting density with the intention of gaining more crop yield per unit area. However, increase in planting density also increases the deleterious effects of intraspecific competition. Crop yield per unit area levels off at a threshold density or can experience a slight decrease (Mead, 1970; Weiner and Freckleton, 2010; Fibich *et al.*, 2014). Knowing the density effects on crop yield and crop quality, the “optimum planting density” is always sought by farmers and researchers to secure optimisation of crop yield under monocultures (Xiao *et al.*, 2006; Kahsay *et al.*, 2014).

1.2. *Interspecific competition and coexistence*

Several theories have been proposed to explain how two species competing for the limiting resources and space can have impact on each other. One of the first such theories is the “competitive exclusion principle”, which hypothesizes that when two species occur in the same environment, one will exclude another due to the requirement for the same resources (Gause, 1932). However, in natural environments, the diversity of coexisting species indicates that “competitive exclusion” is not the main rule. Even though plant species have similar requirements such as space, sunlight, water and soil nutrients, if the competition for all these essential resources is sufficiently weak, two plant species can coexist (Vandermeer *et al.*, 1981; Fargione and Tilman, 2002). The requirement of coexistence is that intraspecific competition must be stronger than interspecific competition (Tilman and Pacala, 1993). Resource partitioning allows species to minimize interspecific competition and is hypothesized to be the reason that allows species to coexist. Spatial partitioning, where species capture resources by occupying different areas and spaces without overlapping home ranges allows species to coexist. For plants, different root depths, heights and canopy structures enable species to acquire soil resources and radiation at different vertical levels (Fargione and Tilman, 2002; Silvertown, 2004) leading to spatial partitioning. Temporal partitioning can occur to avoid strong competition when species vary in their periods of occurrence or with different life history stages exhibited at the same time (Fargione and Tilman, 2002). In addition, different physical requirements for limiting resources can also be important for minimizing competition (Tilman, 1990). For example, if species A is more limited by soil N than P and species B is more limited by soil P than N, the species have potential to coexist.

The mechanisms of plant coexistence provide templates to design and manage agroecosystems. In agricultural systems, intercropping with two crop species has shown in most cases to lead to higher crop yield than that of each of them in monocultures (Lithourgidis *et al.*, 2011). The reason for this outcome may be related to the principle of “resource partitioning” in natural plant communities (Zhang and Li, 2003; Malézieux *et al.*, 2009). Species in mixtures, if selected properly, have potential to exploit space and resources in different proportions and at different time periods, leading to greater use of space and more efficient resource capture than monocultures (Malézieux *et al.*, 2009; Lithourgidis *et al.*, 2011). This phenomenon is known as resource or species complementarity (Hector, 1998). Cereal and legume intercropping systems, for example, are common combinations in which species complementarity is achieved (Belel *et al.*, 2014). In maize (*Zea mays* L.) - pea (*Pisum sativum* L.) intercropping, radiation partitioning is achieved because maize has erect long leaves while pea has fewer prostrate leaves, making it easy to occupy gaps in the maize canopy (Kanton and Dennett, 2008). Leaf morphology of these two species are compatible as they can reduce competition for photosynthetic radiation and intercept it more effectively (Kanton and Dennett, 2008). Dissimilar crops with different and compatible canopy architectures lead to reduction of radiation competition and thus contribute to better crop yield (Belel *et al.*, 2014).

Similarly, root architectures and nutrient requirements of two crops are also determinants of species complementarity. Root placement of maize and bean (*Phaseolus vulgaris* L.) and the different growth rate of roots enable them to uptake soil N and potassium at different depths and time periods, leading to less competition thus higher plant biomass in intercropping (Postma and Lynch, 2012). Mixtures of wheat (*Triticum*

aestivum L.) with bean (*Vicia faba* L.) increase uptake of soil water due to different root distribution and, most importantly, different competitive ability of acquiring soil nutrients: bean is more competitive for Ca and Mg while wheat is more competitive for uptake of P and K (Eskandari, 2011). These studies indicate that the choice of crop species in mixtures based on their morpho-physiological traits is a key for successful intercropping (Belel *et al.*, 2014).

Besides crop selection, planting practices and management also play an important role in successful intercropping (Lithourgidis *et al.*, 2011; Belel *et al.*, 2014). The relative sowing time of component crops is important for the outcome of interspecific competition. In maize-soybean intercropping, maize must be planted later than soybean, since maize rapidly develops tall stems and canopy that can suppress the growth of soybean, which is slower (Addo-Quaye *et al.*, 2011). Therefore, planting slow growing, short plant species before the fast growing, taller and higher leaf area species can balance the competitive ability and benefit both species (Addo-Quaye *et al.*, 2011; Belel *et al.*, 2014).

Similarly, nutrient application influences competition between plant species because it changes soil resource availability (Belel *et al.*, 2014). Some plant species may increase growth rate and produce more canopies with greater N availability while other may not (Wilson and Tilman, 1993). For example, wheat decreases soil N absorption and reduces the development of canopies at high N levels while oilseed rape (*Brassica napus* L.) increases both (Guglielmini *et al.*, 2000). While chemical fertilizers can potentially increase crop yield, it is important to know that in crop mixture systems, the use of these nutrient inputs can change the competitive balance between plant species (Guglielmini *et*

al., 2000; Belel *et al.*, 2014). A successful intercropping system should manage nutrient application in such a way that nutrient use efficiency is optimized between crop species, ensuring that one species is not dominant in the mixture (Belel *et al.*, 2014).

1.3. *Facilitation*

Positive interactions among plants can be defined as the processes by which plants ameliorate harsh environments and increase resource availabilities to the same or other species (Callaway, 1995). If intercropped species are well selected, facilitative interactions can be promoted (Zhang and Li, 2003). In intercropping systems, the common types of mixture are legumes and non-legume species combination due to the capacity of biological nitrogen fixation (BNF) of many species in the family *Leguminosae* (Chapagain and Riseman, 2014; Aminifar and Ghanbari, 2014). The symbiotic bacteria (rhizobia) attach to the root systems of the legumes and form nodules. These rhizobia are able to fix atmospheric N₂ into NH₄, which is then converted to soluble N such as NO₃⁻ and is available to plants (Schubert, 1986). This process enables legumes to enrich the soil N content that is beneficial to themselves and also to their neighbouring plants (Zhang and Li, 2003). For example, intercropping lentil (*Lens culinaris* L.) with barley (*Hordeum vulgare* L.) increases soil N levels through the BNF by the bacteria associated with lentil resulting in greater yield of barley when compared to barley monoculture (Dahmardeh, 2013). In addition to BNF, legumes are found to be able to solubilize and mobilize soil nutrients by acidification, increasing soil P availabilities to their neighbouring plants (Hauggaard-Nielsen and Jensen, 2005). For example, chickpea (*Cicer arietinum* L.) and lupine (*Lupinus albus* L.) can exude carboxylates to dissolve the stable-formed soil P and make it soluble and available to

other plants (Veneklaas *et al.*, 2003). Moreover, it is found that intercropping legumes can alter the microbial communities around the rhizosphere. For instance, the bacterial community structure in the rhizosphere of faba bean and wheat intercropping is different from that of the wheat monoculture (Wang *et al.*, 2007). The activities of these microorganisms can change the soil nutrient availability and benefit plants. He *et al.* (2013) have found that intercropping maize with chickpea and soybean (*Glycine max* L.) changes the rhizobial communities, leading to the enrichment of soil P availability and then increased plant P uptake.

Non-legume species can also have facilitative effects on other plant species. For example, the intercropped oat can prevent pea from lodging by giving the pea a structural support (Kontturi *et al.*, 2011). Lodging increases the possibility of plants to get subsequent diseases and infections and reduces the efficiency of light interception. Therefore, intercropping species with lodging resistant ability can improve the yield and quality of the neighbouring species (Lithourgidis *et al.*, 2011). Another indirect facilitation effect includes reduction of insect pests and plant disease. Lai *et al.* (2011) reported that intercropping tobacco (*Nicotiana tabacum* L.) with garlic (*Allium sativum* L.) reduces the abundance of green peach aphids when compared to monocultures, most likely due to the volatile compounds of garlic. This results in the increase of yield and quality value of the intercropped tobacco.

Facilitative interactions of plants can also occur through the exudation of allelopathic chemicals such as growth regulators. Plant growth regulators are chemical compounds that can alter the dry matter production and the development of plants (Hauggaard-Nielsen and Jensen, 2005). It is found that these compounds can enhance

physiological processes such as seed germination, root growth, leaf expansion as well as chlorophyll accumulation (Hauggaard-Nielsen and Jensen, 2005; Farooq *et al.*, 2013). A recent study indicates that root exudates of onion stimulate the seedling growth of tomato (*Solanum lycopersicum* L.) (Liu *et al.*, 2013).

1.4. Allelopathy

As suggested above, plants produce many secondary metabolites that can have positive or negative effects on other plant species. They can also play a role in defence against herbivores, weeds, and plant pathogens (Itani *et al.*, 2013). Some of these chemicals can directly affect plant germination, growth and development as they can interfere with some basic processes of the receiver plants such as cell division, respiration, photosynthesis and protein synthesis while some indirectly affect plants by changing the soil nutrients and soil microbial activities (Lam *et al.*, 2012; Farooq *et al.*, 2013).

Allelochemicals are released into the environment through various plant tissues including roots, stems, leaves and seeds (Makoi and Ndakidemi, 2012). In crop mixtures, the effects and the amount of allelochemicals released by plants into the ecosystems depend on crop species, cropping or planting practices and the environmental factors such as soil nutrient level, water content and temperature (Batish *et al.*, 2001; Makoi and Ndakidemi, 2012).

Inhibitory effects of allelochemicals on plant growth and germination are reported (Farooq *et al.*, 2013). For example, allelochemicals have been identified in cereal species such as wheat, barley, rice (*Oryza sativa* L.) and sorghum (*Sorghum bicolor* L.) (mainly phenol compounds and alkaloids), which have inhibitory effects on the capability of germination of other legume crops (Książak and Staniak, 2011; Makoi and Ndakidemi,

2012). Likewise, acidic extracts of wheat inhibit root growth of lettuce (*Lactuca sativa* L.) (Lam *et al.*, 2012).

The inhibitory effects of allelochemicals of crops on weeds have also been identified. Sorghum and sunflower (*Helianthus annuus* L.) residues show strong suppression effects on the growth and density of weeds such as wild oat (*Avena fatua* L.) and canary grass (*Phalaris canariensis* L.) (Lam *et al.*, 2012). On the other hand, allelochemicals show promoting effects on growth and germination of other plants. Aqueous extracts of some cereal crops, such as maize and sorghum, stimulate growth of other crops when applied at low concentrations (Farooq *et al.*, 2013). The evidence that root exudates from legumes enhance microbial communities in the soil and indirectly facilitate other plants has been discussed in the previous section. In addition, some plants can detect one another via these allelochemicals and respond to neighbouring plants by spatial avoidance and segregation of root and shoot systems (Chen *et al.*, 2012). The detection and recognition of the neighbouring plant by these allelochemicals regulate the intensity of intra- and interspecific competition (Chen *et al.*, 2012). For example, exposing *Arabidopsis thaliana* to the exudates of other species caused greater lateral root formation than when the plant was exposed to its sibling exudates (Biedrzycki *et al.*, 2010). This suggests that plants may have kin recognition ability through the secretion and sense of some soluble chemicals (Biedrzycki *et al.*, 2010).

Due to the complex allelopathic interactions among crops, the isolation of allelochemicals and the better understanding of their mechanisms of action need to be further investigated (Makoi and Ndakidemi, 2012; Farooq *et al.*, 2013). Studies on plant

performances under intercropping may help find out potential allelopathy between plants in agricultural systems.

1.5. Crop-weed competition

Plants compete for light, water and soil nutrients and decrease the availability of these resources to other plants (Ghanizadeh *et al.*, 2014). Weeds are considered stronger competitors than many crops because of their life-history traits such as taller and erect shoot, planophile leaves, rapid response to shading by adjusting leaf and shoot biomass, fast growth and high root density, fast uptake of soil nutrients and production of allelochemicals (Dunbabin, 2007; Aspasia *et al.*, 2009). For example, the taller habit of smooth pigweed (*Amaranthus hybridus* L.) enables the weed to have greater light interception than lettuce and reduces lettuce growth (Santos *et al.*, 2004). Similarly, common purslane (*Portulaca oleracea* L.) is more efficient in P uptake than lettuce, increasing its competitive advantage against the crop (Santos *et al.*, 2004).

The competitive relationship between plants is not only determined by the biological traits of the species but is also affected by the environmental conditions such as space, light, water and nutrient availabilities and disturbances (Tilman, 1981; Aspasia *et al.*, 2009). It has been reported that fertilizers play an important role in the competitive balance between crops and weeds (Qasem, 2006). The responses of weeds and crops to high levels of fertilizer application greatly vary among species, but many weeds tend to respond better than crop species to high availability of nutrients (Qasem, 2006; Aspasia *et al.*, 2009). A study on carrot (*Daucus carota* L.) and common lamb's-quarters (*Chenopodium album* L.) shows that nutrient availability can affect the competitive interactions between these two species. *C. album* is more competitive than carrot under

relatively low and high nutrient concentrations while under intermediate concentration of nutrients, carrot is more competitive than the weed (Li and Watkinson, 2000).

The outcomes of crop-weed competition are highly affected by the duration of competition. Early emerging species have greater competitive advantages in taking up space and resources (Dunbabin, 2007). The physical occupation of soil space by crop roots may deny weeds further occupation or *vice versa* (Dunbabin, 2007). The early emerging species usually have larger canopies, which can overshadow the late emerging species thus negatively affecting photosynthetic rate, growth, and biomass accumulation (Stagnari and Pisante, 2011).

Other factors affecting competitive ability of crops are density and spatial planting pattern (Aspasia *et al.*, 2009). Increase in crop density and uniformity can suppress weed growth (Olsen *et al.*, 2005; Marín and Weiner, 2014). Increase in crop density is hypothesized to increase the degree of size asymmetric competition (Marín and Weiner, 2014). Bigger plants are usually more competitive in capturing resources. If initial size of the crops is bigger than the weeds, crops have competitive advantages and these advantages are greater if the planting density of the crop is high (Marín and Weiner, 2014). Similarly, spatial uniformity can reduce intraspecific competition among crops and can increase the competitive ability of the crop against weed introduction than clumped distribution due to the better occupancy of space and more efficiency in resource use (Olsen *et al.*, 2005; Marín and Weiner, 2014). In contrast, a clumped planting pattern can result in overcrowding, reducing yield and leaving more space for weed grown (Marín and Weiner, 2014).

2. Effects of crop diversity on weed suppression

Cropping systems with high crop diversity are reported to have less weed infestation problems (Lithourgidis *et al.*, 2011). Intercropping increases plant diversity in the field and reduces weed density and biomass resulting in more stable crop yields when compared to monocultures (Bilalis *et al.*, 2010; Lithourgidis *et al.*, 2011; Corre-Hellou *et al.*, 2011). This phenomenon can be derived back from research about the ecological functions of biodiversity in ecosystems, which suggests that species richness and invasibility are inversely related (Tilman, 1997). Based on this assumption, two possible mechanisms are hypothesised to explain the weed suppression effects in agroecosystems that have diverse assemblages of crops. The “sampling effect hypothesis” states that since diverse systems are more likely to contain one or more competitive species against weeds, these systems are less likely to have weed invasion than in systems with low diversity (Huston, 1997; Fargione and Tilman, 2005). The “complementarity hypothesis” states that systems with greater species diversity are likely to exploit the environment more efficiently in space and time, leaving less available resources to weeds than in lower diversity systems (Fargione and Tilman, 2005).

The evidence for the “sampling effect hypothesis” is reported by Dukes (2002) in a microcosm experiment where an increase in crop species richness did not increase resistance to weeds but if the competitive species, hayfield tarweed (*Hemizonia congesta* DC.) was present, weed growth was suppressed. This study pointed out the importance of the presence of competitive crops in resisting weed invasion (Dukes, 2002). However, another study showed that the competitive resident species (*Schizachyrium scoparium* Michx.) resisted invasive weeds better when it is grown with other resident species

(Fargione and Tilman, 2005). This suggested that both “sampling effect” and “complementarity effect” may simultaneously contribute to the lower invasibility (Fargione and Tilman, 2005; Frankow-Lindberg *et al.*, 2009). In the study, the resident species (*S. coparium*) had higher competitive ability than weeds, owing to its functional traits such as C₄ photosynthesis pathway and higher root growth. However, when *S. coparium* was mixed with other resident species, the mixture reduced soil N at multiple depths, leaving less N for weeds to invade (Fargione and Tilman, 2005). This suggests that complementarity use of resources between crops also plays an important role in resisting weed invasion (Frankow-Lindberg *et al.*, 2009). However, empirical evidence of the functional effects of crop diversity on weed invasion resistance is still limited (Frankow-Lindberg *et al.*, 2009). Are “sampling effect” or “complementarity effect” the most dominant mechanisms in intercropping systems when resisting weeds? Or do they both work at the same time? This requires further investigation into the role of the competitive crop species in its monoculture and how it interacts with other crops in intercropping.

3. Local adaptations of weeds

Rapid evolutionary change in weeds due to human management has been commonly observed (Bommarco *et al.*, 2010). The long-term, repeated agricultural practices, such as crop rotation, mechanical disturbances including harrowing and ploughing and application of chemical inputs like fertilizers and herbicides impose strong selective pressure on the weeds. These anthropogenic disturbances lead some phenotypes to survive while excluding others, causing population genetic shifts and changes in weed community composition over time (Murphy and Lemerle, 2006; Bommarco *et al.*, 2010).

Sufficient heritable genetic variation is the fundamental basis for selection and evolutionary adaptation to environmental change. Genetic variation provides weeds with capacity to enhance survival under disturbances (Guglielmini *et al.*, 2007). Phenotypic changes in life history, plant morphology, seed dormancy and phenology between populations may be an indication of local adaptation to different environments (Murphy and Lemerle, 2006; Guglielmini *et al.*, 2007). To study the genetically based phenotypic differentiation among plant populations, common garden experiments are widely used. In such experiments, samples collected from different populations are raised under common identical environment. In this case, the genetic based phenotypic variation can be observed (Weinig, 2000).

In agricultural systems where crop rotation schedules are stable, weed populations may interact with a single crop species or few crop species in a long term. Under this scenario weed traits that have competitive advantages against these crops or traits that allow weeds to escape competition are selected (Guglielmini *et al.*, 2007). For example, when seeds of velvetleaf (*Abutilon theophrasti* L.) collected from two different populations (long term maize and soy cultivation field vs. natural weedy area) were planted under the same controlled condition in the greenhouse, different elongation times were found (Weinig, 2000). This suggested that populations of velvetleaf in two isolated locations encountered different interspecific competitors and that caused genetic differentiation for certain morphological and life-history characters (Weinig, 2000). Similarly, a greenhouse study using a common garden experiment followed by genetic analyses (amplified fragment length polymorphism markers) demonstrated differentiation in populations of creeping thistle (*Cirsium arvense* L.) in terms of its quantitative

characters among plants from agricultural, semi-natural and natural habitats (Bommarco *et al.*, 2010). Specifically, the population of creeping thistles from the natural habitat had the largest numbers of shoots and roots, tallest, and fastest growth, indicating that selective pressures in the natural habitat are greater and increase the competitive ability of the plant (Bommarco *et al.*, 2010).

In conventional agriculture, weeds may adapt to the application of long term usage of herbicides and fertilizers. Herbicide resistance has been reported in weed populations (Murphy and Lemerle, 2006). The use of herbicides not only favours tolerant phenotypes but also alters seed germination of weeds because those emerging later can escape the early weed controls (Murphy and Lemerle, 2006). Similarly, the use of fertilizers can lead weeds to become more tolerant to high nutrient levels (Ryan *et al.*, 2010; Murphy and Lemerle, 2006). For example, a greater mortality of velvetleaf and giant foxtail (*Setaria faberii* Herrm.) seeds was observed in soil with high N levels (Davis, 2006). Seeds of some weed species are not able to survive high soil nutrient levels (Davis, 2006). Applications of fertilizers also select weed traits indirectly. Soil with high nutrient levels increases the growth rate and competitive ability of crops, which means that fertilization also favour weeds that can survive such competition (Murphy and Lemerle, 2006). Traits such as the shade intolerance or capability of increase in shoot height may enable weeds to adapt (Murphy and Lemerle, 2006).

Physical disturbances such as tillage and harvesting can also act as selective pressures on weeds. Weeds that mature and set seeds earlier before the harvesting can leave their seeds in the seed bank and remain in the field while seeds of late maturing weeds are probably removed with mechanical harvesting (Murphy and Lemerle, 2006).

Weed population shifts in agriculture systems are the result of complex interactions of all these agricultural practices thus it is difficult to isolate the single factor that causes the evolutionary change of weeds. However, comparison of weed populations from microsites with relatively clear and distinguished disturbance regimes can provide insight into the selection mechanisms (Bommarco *et al.*, 2010). For example, creeping thistle populations in conventional farms have lower genetic variability than in organic farms probably due to the use herbicides acting as a stronger selective pressure on the weed in the conventional farm than in the organic farm (Bommarco *et al.*, 2010). However, other than herbicide use, the potential evolutionary consequences of other agricultural practices are still not completely known (Bommarco *et al.*, 2010).

4. Greenhouse studies on plant-plant interactions

In natural plant communities, the complexity of biotic and abiotic factors increases the difficulties of studying plant interactions (Gibson *et al.*, 1999). Fluctuations of temperature, soil conditions and the presence of insects and diseases distract from the competition effects and outcomes. Conversely, greenhouse experiments minimize the extrinsic variability and allow the impact of some factors to be measured in isolation (Freckleton and Watkinson, 2000). In those conditions, it is possible to control the number of plant species, spatial patterns and physical environments such as soil fertility or moisture. In addition, the repeatability and the flexibility to different statistical design also make greenhouse studies appealing (Gibson *et al.*, 1999). Of course, the lack of realism restricts the generalisation of the results found in greenhouse studies and long term greenhouse experiments on perennial plants are difficult to conduct due to the restriction of space (Gibson *et al.*, 1999). The aims of greenhouse experiments are either

to use the results to generate certain hypotheses that can be further tested in field conditions or to test some conditions that can be used for vegetable growth in greenhouses (Freckleton and Watkinson, 2000).

Greenhouse experiments used to test techniques for transferring into the field require understanding of field conditions such as planting density, sowing time, and phenology where crops are to be grown. Ideally, the use of standardized experimental designs and comparable measurements are advantageous if a researcher wishes to compare greenhouse and field studies (Gibson *et al.*, 1999; Freckleton and Watkinson, 2000).

Internationally, there is a considerable increase in greenhouse agriculture for producing vegetables (www.ishs.org). Because conditions are more controlled but greenhouse space is limited, the understanding of plant-plant interactions is becoming ever more important. This thesis has been initiated partly with this new reality in mind.

Two common experimental designs that have been used to compare plant interactions under monocultures vs. polycultures both in the greenhouse and field conditions are the replacement series (substitutive) design and the additive design. In replacement series design, the densities of species A and species B in their monocultures are their optimum planting densities. A mixture with half of the densities of each species is used. This design is suitable to investigate yield advantage of mixtures with two or more component crops in intercropping studies and also to investigate to what degree resource partitioning might contribute to a yield advantage (Sobkowicz and Podgórska-Lesiak, 2007).

In additive design, the densities of species A and species B in their monocultures are their optimum planting densities, while the mixture is the combination of pure stand plant densities of both species. This design is widely used in crop-weed competition studies because it is similar to the situation in agroecosystems where weeds emerge in the established crop fields, adding their plants to the standing crops and starting to compete for resources (Sobkowicz and Podgórska-Lesiak, 2007). In this situation the crop is planted at optimum density, while weed densities are usually similar to that observed in the agricultural field (Sobkowicz and Podgórska-Lesiak, 2007). In this research, both replacement and additive design were used to study crop-crop and crop-weed interactions.

5. The ecology of the studied species

Species with different morphological and physiological traits potentially enable them to achieve resource partitioning in intercropping. In this study, *Allium cepa* and *Phaseolus vulgaris* were used as test species for intercropping. In addition, in order to better understand weed invasion, two of Canada major weed species were selected: *Chenopodium album* and *Amaranthus hybridus*. In this section, these four species are described in terms of ecology and potential use or impacts in agriculture.

5.1. Bulb onion (*Allium cepa*)

Bulb onion is a biennial and cross-pollinated plant belonging to family *Alliaceae*. It is one of the most important vegetable crops worldwide (Qasem, 2006). Evidence shows that onions originated in the mountainous regions of central Asia where the climate is warm and dry (Griffiths *et al.*, 2002). The morphology of onions allows them to adapt in such environments. Onion bulbs contain water and carbohydrates such as glucose, fructose and fructans and these constitute about 80% of the shoot weight

(Benkeblia *et al.*, 2004). The bulb enables onion to get through arid periods. Likewise, the upright, cylindrical leaves help onion limit the rise of leaf temperature during hot days (www.onionsaustralia.org.au). Onion has a relatively slow growth rate, shallow (25 to 50 cm) and poorly branched root systems (Weaver and Bruner, 1927; Thorup-Kristensen, 1999). After germination, the primary root will grow downwards and grow about 0.2 mm per day (Thorup-Kristensen, 1999). These characteristics make onion a weak competitor for sunlight, water and soil nutrients (Qasem, 2006; Patel *et al.*, 2012). Thus, weed infestation is the major problem in onion fields. *C. album*, for example, is one of the most common weed species found in onion cropping fields (Mennan and Isik, 2003). Yield loss of onion due to weed infestation ranges from 40 to 80% (Prakash *et al.*, 2006; Channapagoudar and Biradar, 2007). To avoid yield loss, direct-seeded onions must remain weed-free for 40-56 days after emergence (Gazdag-Torma, 1997; Patel *et al.*, 2012).

Most onion cultivars are sensitive to temperature. The optimum environment for onion growth is a day/night temperature 25 /18 °C with an 11-12 hour photoperiod (Zena, 2008). Although onion is able to survive arid conditions, an adequate supply of water is required for a good yield (Griffiths *et al.*, 2002). In addition, insufficient N fertility can inhibit bulb maturation and decrease yields (Coolong *et al.*, 2004). Recommended content of N in the field for its growth varies between 157 and 314 kg/ha depending on soil conditions and cultivars (Coolong *et al.*, 2004). Phosphorus deficiencies also reduce root and leaf growth, bulb size and yield and can also delay maturation (Rizk *et al.*, 2012). Onion has been intercropped with lettuce (DeHaan and Vasseur, 2014) and cucumber (Zhou *et al.*, 2011) and facilitative effects were found on the growth of these two crops.

The mechanisms of the facilitation of onion on other crops are not fully known, but it is probably because its root exudates change the soil microbial activities and nutrient availability (Zhou *et al.*, 2011).

5.2. Yellow wax bean (*Phaseolus vulgaris*)

Yellow wax bean is an annual and self-pollinated plant belonging to family *Leguminosae*. It is widely cultivated all over the world for its pods and seeds as a source of calories and dietary proteins (Yadegari *et al.*, 2010). Yellow wax bean has an upright habit with an erect stem and branches which have 3 to 7 trifoliate leaves (Graham and Ranalli, 1997). The high overall leaf area and planophile leaves of the bean make it a strong competitor for sunlight, especially in the early growth stages (Bilalis *et al.*, 2010). Yellow wax bean has horizontal well-branched and deeper root systems (> 100 cm) than onion (Weaver and Bruner, 1927). Roots of the bean can be inoculated by N-fixing bacteria. However, yellow wax bean is considered to be a weak N fixer compared to other legumes (Yadegari *et al.*, 2010). Amounts of N fixed by inoculated plants range from 27 to 72 kg/ha depending on the bacterial strains and cultivars (Graham and Ranalli, 1997). Nodulation of the bean is also limited by environmental factors such as N fertilization, temperature and soil moisture content (Yadegari *et al.*, 2010).

Even though yellow wax bean has a strong and rapid emerging canopy, weed problems are reported to cause yield loss. *C. album* and redroot pigweed (*Amaranthus retroflexus* L.) are major weeds found in bean fields (Stagnari and Pisante, 2011). Fields need to be free of weeds between 11 and 29 days after bean plants emerge to prevent yield loss (Stagnari and Pisante, 2011). The major reasons for weed interferences in most legume fields are low planting densities and wide-row planting methods

(Dusabumuremyi *et al.*, 2014). Optimum planting density for yellow wax bean varies depending on cultivars. Research has also reported low (6 plants /m²) and high planting density of the species (43 plants /m²) (Teasdale and Frank, 1983).

Yellow wax bean is a cold season plant. Day temperatures > 30°C can inhibit flowering and reduce seed yield (Siddique and Goodwin, 1980; Muasya *et al.*, 2008). In addition, even though yellow wax bean is able to fix N, fertilizers are often used with rates to about 60 kg N/ha to ensure a good yield (Graham and Ranalli, 1997). Yellow wax bean requires adequate P for vigorous growth but beans can tolerate low levels of soil P. Yellow wax bean enhances rhizosphere acidification through the release of acid phosphatase and protons which can hydrolyse the organic P compounds from non-absorbable to absorbable inorganic P (Graham and Ranalli, 1997; Kouas *et al.*, 2009). Many legume species are successfully intercropped with cereals. When *P. vulgaris* was intercropped with maize (Latati *et al.*, 2013) and durum wheat (Li *et al.*, 2008) soil N and P availabilities and nutrient uptake in neighbouring plants (maize and wheat) increased.

5.3. Common lamb's-quarters (*Chenopodium album*)

C. album is an annual weed belonging to family *Chenopodiaceae* (Bassett and Crompton, 1978). It is a broad-leaved weed with deep tap roots, profuse branching and high fecundity. It reproduces rapidly through self and cross pollination. According to the Ontario Ministry of Agriculture (www.omafra.gov.on.ca), *C. album* is widespread throughout Canada and grows in the places where the soil is highly disturbed (cultivated fields, pastures, wasteland, roadsides, gardens). The weed is also widely distributed across Asia, Europe and even Arctic regions.

Stems of *C. album* can grow up to 300 cm in height and are highly branched. The effect of *C. album* on crop growth can be severe in the early stages due to its rapid elongation (Bassett and Crompton, 1978). The weed has shade-avoiding adaptive traits, which allow it to enhance stem elongation, develop more shoot biomass and more leaf area to prevail in sunlight competition (Mahoney and Swanton, 2008). Production of a large number of seeds (> 600,000 seeds per plant) makes this weed hard to control and exclude from the seed bank (Bassett and Crompton, 1978).

C. album can grow on almost any type of soil and in a wide range of pH, from strongly acid to alkaline (Bassett and Crompton, 1978). In addition, competitiveness of the weed is highly responsive to N level as biomass of *C. album* increases significantly as soil N increases (Blackshaw *et al.*, 2003). Moreover, *C. album* is shown to take up large amounts of phosphate at early and late stages of its growth cycle (Bassett and Crompton, 1978). Negative allelopathic effects have been observed on the shoot and root growth and germination of crops such as soybean and wheat (Alam *et al.*, 2002; Namvar *et al.*, 2009).

5.4. Smooth pigweed (*Amaranthus hybridus*)

Smooth pigweed is an annual, self-pollinated and broadleaf weed belonging to family *Amaranthaceae* (Costea *et al.*, 2004). According to the Ontario Ministry of Agriculture (www.omafra.gov.on.ca), *A. hybridus* occurs in crop fields, gardens, and waste places in southern Ontario.

A. hybridus has an erect or bushy habit with alternate and petiolate leaves on stems. The weed grows to at least 50 cm tall with some growing to nearly 300 cm in height (Sellers *et al.*, 2003). Like *C. album*, *A. hybridus* has high level of fecundity. A single mature plant can produce up to 250,000 seeds and this makes the weed difficult to

manage (Massinga *et al.*, 2001; Sellers *et al.*, 2003). Compared to many warm-season vegetables, *A. hybridus* grows faster and is a strong competitor when grown with shorter crops such as broccoli (*Brassica oleracea* L.) and snap bean (Massinga *et al.*, 2001). Unlike *C. album*, *A. hybridus* exhibits a C₄ photosynthesis pathway. C₄ plants have higher photosynthetic rates under high temperatures and light intensity (Costea *et al.*, 2004). C₄ plants also have lower CO₂ compensation point, less photorespiration and higher N use efficiency when compared to C₃ plants (Costea *et al.*, 2004). N application stimulates the weed and causes rapid growth. *A. hybridus* is also a large consumer of soil P. It assimilates P resulting in increased P content in plant tissues but without increased plant biomass (Costea *et al.*, 2004; Santos *et al.*, 2004). The weed can tolerate a broad range of soil types, textures and pH levels (Costea *et al.*, 2004). Shoot extracts of *A. hybridus* inhibit bean vegetative growth and cause grain yield loss (Amini and Ghanepour, 2013). It has negative allelopathic potential to germination of spinach (*Spinacia oleracea* L.), bean and lettuce (Hakimi Rezaei, 2013).

6. Objectives and hypotheses

In the previous sections, current knowledge regarding plant-plant interactions was explained. Ecological concepts such as resource partitioning, facilitation and resistance to invasion remain concepts to better understand especially under greenhouse conditions. Therefore, the overall objective of the study was to investigate the effects of interactions between onion and yellow wax bean under monoculture and intercropping conditions with or without the presence of weeds. More precisely, the three main objectives were as follows:

Objective 1: To investigate whether the growth and yield of onion and yellow wax bean differ between monocultures (intraspecific interaction) and intercropping (intraspecific interaction + interspecific interaction).

Hypothesis: onion and yellow wax bean under intercropping would have greater growth and yield than under monoculture.

Predictions: Due to different leaf and root architectures of the two crop species, resource partitioning would be achieved in intercropping. Therefore, intensity of interspecific competition between the two crops would be lower than the intraspecific competition in their own monocultures.

Objective 2a: To examine the growth of two weeds (either *C. album* or *A. hybridus*) under onion monoculture, yellow wax bean monoculture and onion-yellow wax bean intercropping.

Hypothesis: weeds would not perform well in onion-yellow wax bean intercropping as in either onion or yellow wax bean monocultures and that *A. hybridus* would perform better than *C. album*.

Predictions: Due to different leaf and root architectures of the two crop species, the “complementarity effect” would be achieved. So, physical space and resources in above- and belowground would be used more completely by the crops in intercropping and would leave less space and resources to the weeds to grow. In two monocultures, yellow wax bean would suppress weeds better than onion due to the strong canopy of the bean. It was expected that due to the C₄ photosynthesis pathway, *A. hybridus* would perform better than *C. album* in the various monocultures and intercrop conditions.

Objective 2b: As the counterpart of the previous objective, this objective aimed to compare growth and yield of the two crops with and without the presence of weed (either *C. album* or *A. hybridus*) when grown under intercropping or monoculture conditions.

Hypothesis: crop growth and yield in intercropping would be less affected by the presence of weeds than those in monoculture.

Predictions: As intercropping was expected to suppress weeds better than monocultures, crops growth and yield in intercropping should be more stable and less affected if weeds were present. In addition, yellow wax bean monoculture would be less affected by the presence of weeds than onion monoculture because bean is more competitive in sunlight capturing against weeds.

Objective 3: To investigate how growth and morphological traits of *C. album* from either an organic farm or a conventional farm would differ using a common garden experiment.

Hypothesis: *C. album* plants from the conventional farm would have better growth and different morphological traits than do *C. album* plants from the organic farm in the common garden experiment.

Predictions: Use of chemical fertilizers in the conventional farms would probably have led to weeds growing faster and bigger than those in the organic farms. Thus, in a long term, *C. album* plants from conventional farms would have adaptive traits associated with better competitive ability (e.g. larger and higher shoot). Under controlled conditions (common garden), it was expected that plants from a conventional farm would grow individually larger than those from an organic farm.

Materials and Methods

Experiment No. 1. *Measurement of crop performance under monoculture vs. intercropping conditions*

Study site

The experiment was conducted between September 2013 and June 2014 at the greenhouse in Cairns Building, Brock University. The environmental conditions in the greenhouse were controlled with temperature set at 24°C in daytime and 18°C at night. Photoperiod was 14 hours of daylight at an intensity of 400 W/m². Relative humidity was maintained at 65%.

Plant materials

The cultivar of the bulb onion (*A. cepa*) was Alpine - 210V (Stokes Canada). This cultivar matures within 75 days. Yellow wax bean (*P. vulgaris*) cultivar used in the experiment was Sunburst - 10J. This cultivar matures within 51 days. The selection of these cultivars was due to their short maturity time, seed germination rate and general growth performance. All plants were planted in Sunshine Mix #1 soil (Table A8, Appendix).

Experimental design

The experimental design used in the study was a randomized block design with two experimental runs due to limited space in the greenhouse. Experiments were carried out using five treatments (Figure A1, Appendix): i) monoculture of eight onions (treatment called M8O; n=10); ii) monoculture of sixteen onions (M16O; n=17); iii) monoculture of six yellow wax beans (M6B; n=11); iv) monoculture of twelve yellow wax beans (M12B; n=15); and, v) intercrop of eight onions and six yellow wax beans

(IOB; n=18). Replicates were planted in pots of 30 cm length \times 30 cm width \times 25 cm depth, representing microcosms of row intercropping in the field. The sowing depth and space between seeds were suggested by the seed company.

Onion seeds were sown at a depth of 2 cm. In the M16O treatment, 16 seeds were planted in four rows, four seeds per row, i.e. 5 cm apart in row with 6 cm between rows. In the M8O treatment, eight seeds were planted in two rows, four seeds per row, 5 cm apart in row and 12 cm were left between rows.

Yellow wax bean seeds were sown at a depth of 2.5 cm. In the M12B treatment, twelve seeds were planted in four rows, three seeds were planted per row, i.e. 7.5 cm between seeds and 6 cm between rows. In the M6B treatment, six seeds were planted in two rows. Each row contained three seeds planted at 7.5 cm distance with a 12 cm between rows.

In the IOB treatment, eight onion seeds were planted in two rows, four seeds per row with 12 cm apart between rows. Then six yellow wax bean seeds were planted into two rows between the rows of onions. In the IOB treatment, since onion is slow growing (usually planted in the spring), yellow wax bean seeds were sown 20 days after emergence of onions to prevent the wax bean canopy from affecting the survival of onion.

Plants were regularly watered as soon as the soil surface became dry and plants were fertilised using PlantProd All Purpose Fertilizer (20-20-20) once a month, according to the instructions from the seed company (Table A9, Appendix).

Harvest and measurements

Onions were harvested after 75 days and yellow wax bean after 51 days (as suggested by the seed company). At harvest, the following measurements were taken for

each individual plant: 1) plant height; measured from the base of the shoot to the top of the shoot for wax beans or from the bulb to the tallest leaf for onion; 2) aboveground fresh weight including shoots, leaves and pods for yellow wax beans and leaves and bulb weight for onions; and 3) leaf area for all individuals of yellow wax beans (LI-3100C portable leaf area meter; Li-Cor, Lincoln, NE). Plants were then dried at 50°C for at least two weeks and dry weights of the different parts (as above) of the plants were recorded.

Data analyses

The Relative Yield Total (RYT) (de Wit, 1960) was used as an indicator of the extent to which crop components shared common resources. The formula is the sum of the relative yield of two component crops:

$$RYT = \frac{I1}{M1} + \frac{I2}{M2}$$

where M1, M2 are total aboveground dry weight of onion and yellow wax bean per unit area in monoculture and I1, I2 are total aboveground dry weight of onion and yellow wax bean per unit area in intercropping. A RYT value equal to 1.0 indicates component crops in the mixture fully share the same limiting resources. Values between 1.0 and 2.0 would indicate that component crops are partially sharing limiting resources. Values < 1.0 would indicate that the component crops suppressed each other not only through resource competition but other effects such as allelopathy. Values > 2.0 would indicate that at least one component stimulates the growth of the other (Tofinga, 1993).

The Relative Interaction Index (RII) (Armas *et al.*, 2004) was also used to quantify the interactions between the two crops. Aboveground total fresh weight was used to substitute into the following formula:

$$RII = \frac{M_w - M_o}{M_w + M_o}$$

where M_w is the sum of aboveground individual fresh weight of onion or yellow wax bean in intercropping treatment and M_o is sum of aboveground individual fresh weight of onion or yellow wax bean in monoculture treatment. RII has values ranging from [-1, 1]. If RII is 0, it indicates neutral interactions, while values < 0 indicate competition and values > 0 indicate facilitation (Armas *et al.*, 2004).

All growth variables of plant individuals (plant height, total above ground fresh/dry weight, onion leaf fresh/dry weight, yellow wax bean shoot fresh/dry weight, onion bulb fresh/dry weight, yellow wax bean pod fresh/dry weight, yellow wax bean leaf area) and plant yield per pot (sum fresh weight of onion bulbs/bean pods) were tested for significant differences using a general linear model analysis of variance due to the unbalanced design. Before testing, all variables were checked for normality. Some variables were \log_{10} transformed (onion dry leaf and yellow wax bean dry shoot weights) before the analysis of variance to meet the needs of normality. Tukey Honestly Significant Difference (HSD) or Dunnett T3 *post hoc* tests were used following the analysis of variance if significant differences were found. HSD was used when the homogeneity of the data was satisfied (all growth variables and bulb yield of onion; height, fresh/dry shoot weights, fresh pod weight of yellow wax bean). Otherwise,

Dunnett T3 was used (dry pod weight, total aboveground fresh/dry weight and pod yield of yellow wax bean bean). Preliminary tests showed that there were no experimental run or block effects and therefore data of both runs were analysed together. Statistical tests were performed using SPSS version 21.0. A value of $p=0.05$ was used for all comparisons. Figures and tables shown in the results contain the original mean values without transformation.

Experiment No. 2. *Measurement of crop-weed interactions under onion and yellow wax bean monocultures and intercropping*

Plant materials

The experiment was conducted in the same greenhouse as Experiment No. 1 using the same environmental conditions. The crop species and cultivars used in this experiment were the same as in Experiment No. 1. Weed species used were common lamb's-quarters (*C. album*) and smooth pigweed (*A. hybridus*). Large mature individuals (containing hundreds of seeds) of *C. album* and *A. hybridus* were collected from two farms of the Niagara region in 2013. One of the farms was an organic farm located in Lincoln and had been under organic farming for more than 10 years. This farm was used to grow onion, lettuce, cruciferous crops (e.g. turnip, broccoli, cabbage, etc.) as well as squash and pumpkin. The second site was a conventional farm located on Lakeshore Road in Niagara on the Lake that cultivated kale, squash and pumpkin for several years and had used chemical fertilizers and herbicides for years.

Three mature plants of *C. album* from the organic farm were selected and named CO1, CO2, CO3 as well as three mature individuals collected from a conventional farm (named as CC1, CC2, CC3). Similarly, three mature plants of *A. hybridus* coming from

the same organic farm were used and named PO1, PO2, PO3 (due to poor germination rate, *A. hybridus* mature individuals from the conventional farms were not used).

Seeds from each mature plant were extracted and kept separately. For the start of this experiment, seeds from each plant were planted in separate trays in the same soil as the previous experiment. After germination, seedlings relatively the same size (about 4th leaf stage, 5 cm high) were transplanted into the treatment pots where crops were already growing. This was to mimic the plant growth schedule in the fields where crops were growing before weed introduction.

Experimental design

To investigate weed growth of two weed species (either *C. album* or *A. hybridus*) under different conditions (M16O, M12B, IOB and the control), an additive method was used. Four weed plants of either *C. album* or *A. hybridus* were transplanted into pots where crops were already growing or without crops. So four basic treatments were conducted: i) M16O with four weed plants; ii) M12B with four weed plants, iii) IOB with four weed plants and, iv) four weed plants alone (control).

Four weed plants per pot were from the same seed parent. So in each basic treatment, weed plant performance from the nine seed parents (e.g. PO1, CO1, etc.) were tested separately. The treatment “M16O with four weed plants” for example, contained nine sub-treatments (nine replicates for each): M16O+4PO1, M16O+4PO2, M16O+4PO3, M16O+4CO1, M16O+4CO2, M16O+4CO3, M16O+4CC1, M16O+4CC2, M16O+4CC3.

When analyzing the data, weed performance in a species level (either *C. album* or *A. hybridus*) under different conditions (M16O, M12B, IOB) were first tested, regardless of which seed parents they were from. On the other hand, crop performance in treatment:

i), ii) and iii) was compared to that in treatments from Experiment No. 1: crop monocultures (M16O, M12B) and intercropping (IOB) without weeds. This was to investigate how crop growth and yield would be affected with or without the presence of weeds.

Secondly, performance of weeds from different parents (PO1, PO2, PO3, CO1, CO2, CO3, CC1, CC2 and CC3) under different conditions (M16O, M12B, IOB and the control) were analyzed. This was to investigate if weeds would exhibit different morphological response within a population (either organic or conventional) and between two populations (organic vs. conventional).

Planting

Crop monoculture and intercropping pots were set up as in Experiment No. 1. Weeds were transplanted into onion monoculture pots 25 days after onion emerged and transplanted into bean monoculture pots 5 days after the bean emerged. For intercropping (IOB) with weed treatments, six beans were sown when eight onions already emerged for 20 days. Five days after, weeds were transplanted into the pots (this transplantation and sowing sequence were to try to mimic the actual agricultural situations where usually weeds emerge after the crops, i.e. different times during the growing season). In each pot, four weed individuals were transplanted 10 cm apart to mimic the weed density (44 individuals /m²) observed on the farms and where and when they were collected on the farms. Plants were regularly watered once a day and plants were fertilized using PlantProd All Purpose Fertilizer (20-20-20) monthly.

Harvest and measurements

Onions were harvested after 75 days and yellow wax bean after 51 days as was done in Experiment No. 1. At harvest, the same variables were measured for crops as was done in Experiment No. 1. For weeds, variables measured included 1) plant height; measured from the base of the shoot to the top of the shoot; 2) total aboveground fresh weight including shoots, leaves and seeds and 3) leaf area using LI-3100C portable leaf area meter (Li-Cor, Lincoln, NE). Plants were then dried at 50°C for at least two weeks and dry weights of the different parts of the plants were measured.

Data analyses

All growth variables of crops and weeds were tested for significant differences using a general linear model analysis of variance on SPSS version 21.0. The analysis procedures were the same as those in Experiment No. 1. Preliminary tests showed that there were no experimental run or block effects and therefore data of both runs were analysed together. Figures and tables shown in the results contain the original mean values without transformation.

Experiment No. 3. *Measurement of phenotypic trait variation of weeds from the organic and conventional farms*

Weed plants from different seed parents were also planted under “one plant per pot” condition (non-competitive environment): seedlings (n=10) from each parent plant were transplanted into 10 cm radius × 25 cm height pots and grown for 55 days. Each pot contained only one seedling (no competition). At the harvest time, measurements were the same as Experiment No. 2 for weeds. Data analyses (analysis of variance) compared differences among plants within population (either organic or conventional) and between the two populations (organic vs. conventional).

Results

Crop performance under monoculture vs. intercropping conditions

The RYT value was 1.3, indicating that the intercrop had yield advantages than the monoculture. Moreover, the result of RII was that yellow wax bean on onion was 0.35 and onion on yellow wax bean was -0.21, suggesting a facilitative effect on onion but a negative effect on yellow wax bean.

In general, onions in intercropping grew better than in monocultures. Mean individual total aboveground fresh/dry weights of onions were significantly greater in intercropping (IOB) than in monocultures (Figure 1). Onions grown in sixteen-onion monoculture (M16O) had significantly greater mean individual total aboveground fresh weight than those grown in eight-onion monoculture (M8O) (Figure 1A). No significant difference was found in mean individual total above ground dry weight between two monocultures (Figure 1B).

Similarly, onions in IOB had significantly greater individual fresh/dry leaf and bulb weights than in monoculture (Table 1). When comparing the two monocultures, onions in M16O had significantly higher mean individual fresh weight of leaves than those in M8O, while no difference in mean individual dry weight of leaves was observed between two (Table 1). Conversely, mean individual dry weight of onion bulbs in M16O was significantly higher than that in M8O, while fresh bulb weights of both monocultures did not significantly differ (Table 1). Individual plant height in IOB was significantly higher than that in monocultures (Table 1). However, plant height between the two monocultures was not significantly different. Intercropped onions gained significantly

higher fresh bulb yield than those in M8O monoculture but did not differ from the fresh bulb yield gained in M16O monoculture (Table 1).

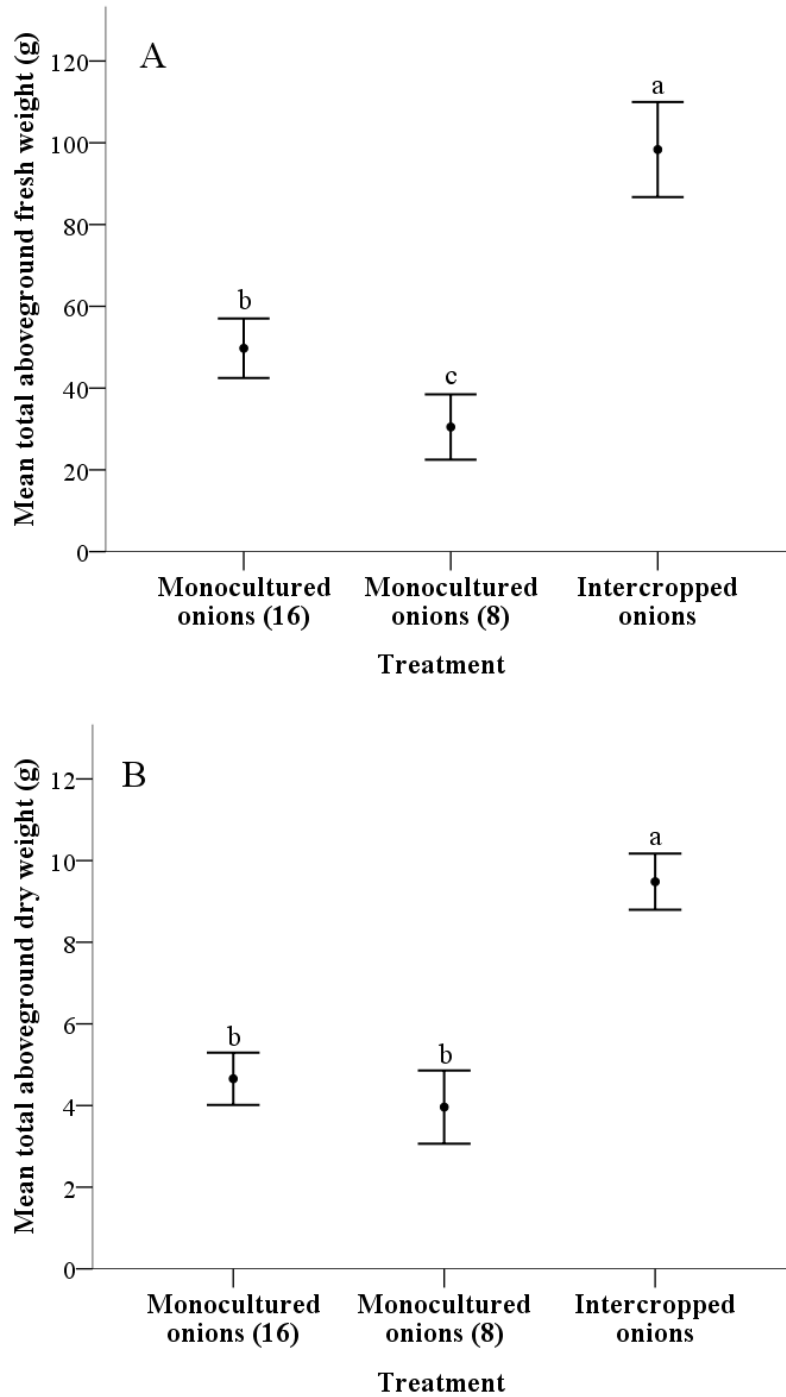


Figure 1. Mean individual total aboveground A) fresh and B) dry weight of onions under two monocultures (sixteen onions per pot, M16O and eight onions per pot, M8O) and under intercropping with yellow wax beans (eight onions with six beans per pot, IOB). Significance is indicated by letters (a, b, c) above the standard error bars. (A: $df=2$, $MS=17951.7$, $F=49.0$, $p<0.001$; B: $df=2$, $MS=141.09$, $F=72.26$, $p<0.001$).

Table 1. Variables measured on onions under monocultures (sixteen onions per pot, M16O and eight onions per pot, M8O) and under intercropping with yellow wax bean (eight onions with six beans per pot, IOB). Significant differences among treatments are indicated by letters in superscript (a, b, c). Mean values (\pm standard error) are the original values without transformation.

Variables	Monoculture onions (M16O)	Monoculture onions (M8O)	Intercropped onion with yellow wax beans (IOB)	F	P
Individual fresh weight of leaves (g)	27.65 \pm 2.58 ^b	8.49 \pm 1.06 ^c	45.05 \pm 4.45 ^a	23.19	<0.001
Individual dry weight of leaves (g)	2.42 \pm 0.26 ^b	2.92 \pm 0.39 ^b	5.58 \pm 0.32 ^a	32.60	<0.001
Individual fresh weight of bulb (g)	22.08 \pm 1.70 ^b	21.99 \pm 3.67 ^b	53.30 \pm 2.61 ^a	54.04	<0.001
Individual dry weight of bulb (g)	2.23 \pm 0.12 ^b	1.03 \pm 0.96 ^c	3.90 \pm 0.85 ^a	77.76	<0.001
Individual height (cm)	52.7 \pm 2.08 ^b	45.81 \pm 3.58 ^b	62.20 \pm 2.46 ^a	9.19	<0.001
Fresh bulb yield (tonnes/hectare)*	38.56 \pm 3.10 ^a	19.33 \pm 3.23 ^b	46.67 \pm 2.33 ^a	53.41	<0.001

*Fresh bulb yield was sum of individual fresh bulb weight per unit area. The unit was changed to tonnes/ha for better comparison with the literature.

Mean total individual aboveground fresh weight of yellow wax beans in intercropping (IOB) was significantly lower than that in twelve-bean monoculture (M12B), while mean total individual aboveground dry weight of intercropped beans was significantly lower than both monocultures (Figure 2). When only comparing the two monocultures, yellow wax beans in M12B had significantly higher mean total individual aboveground fresh weight than in six-bean monoculture (M6B). Mean total individual aboveground dry weight between two monocultures was not different (Figure 2).

Mean individual dry shoot and pod weights of yellow wax beans were significantly lower in IOB than in both monocultures, but mean individual fresh shoot and pod weights in IOB were only lower than those in M12B (Table 2). Comparing the two monocultures, M12B had significantly greater mean individual fresh/dry shoot weights than M6B, while mean individual fresh/ dry pod weights between them were not different (Table 2). The mean individual plant height of yellow wax beans in IOB was significantly lower than that in M12B, but was significantly higher than that in M6B (Table 2). Mean individual leaf area of yellow wax beans in M12B was significantly higher than that in both IOB and M6B (Table 2). Fresh pod yield in IOB was significantly lower than that in M12B but not significantly different from that in M6B (Table 2).

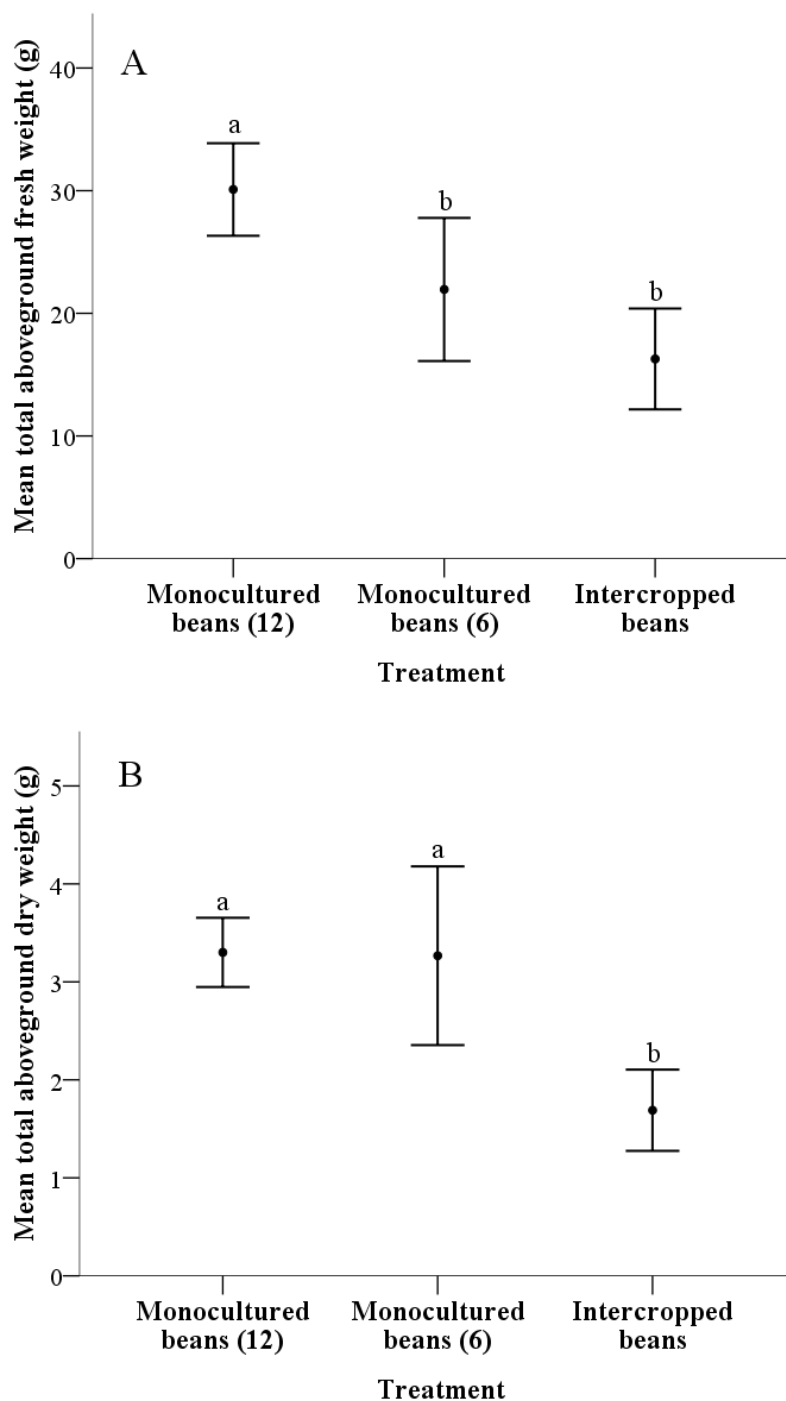


Figure 2. Mean individual total aboveground A) fresh and B) dry weight of yellow wax beans under two monocultures (twelve beans per pot, M12B and six beans per pot, M6B) and under intercropping with onions (six beans with eight onions per pot, IOB). Significance is indicated by letters (a, b, c) above the standard error bars (A: $df=2$, $MS=726.78$, $F=11.12$, $p<0.001$; B: $df=2$, $MS=13.38$, $F=14.17$, $p<0.001$).

Table 2. Variables measured on yellow wax beans under monocultures (twelve beans per pot, M12B and six beans per pot, M6B) and under intercropping with onions (six beans with eight onions per pot, IOB). Significant differences among treatments are indicated by letters in superscript (a, b, c). Mean values (\pm standard error) are the original values without transformation.

Variables	Monoculture yellow wax beans (M12B)	Monoculture yellow wax beans (M6B)	Intercropped yellow wax beans with onions (IOB)	F	P
Individual fresh weight of shoots (g)	18.08 \pm 1.02 ^a	12.48 \pm 1.26 ^b	9.97 \pm 1.16 ^b	13.53	<0.001
Individual dry weight of shoots (g)	2.40 \pm 0.40 ^a	1.68 \pm 0.18 ^b	1.19 \pm 0.13 ^c	22.03	<0.001
Individual fresh weight of pods (g)	12.02 \pm 0.96 ^a	9.47 \pm 2.00 ^{ab}	6.30 \pm 0.94 ^b	6.64	<0.05
Individual dry weight of pods (g)	0.90 \pm 0.07 ^a	1.58 \pm 0.35 ^a	0.50 \pm 0.10 ^b	10.35	<0.05
Individual height (cm)	33.50 \pm 0.76 ^a	20.09 \pm 0.83 ^c	25.90 \pm 1.81 ^b	20.09	<0.001
Individual leaf area (cm ²)	495.79 \pm 16.87 ^a	269.30 \pm 24.68 ^b	292.09 \pm 20.54 ^b	343.00*	<0.001
Fresh pod yield (tonnes/hectare)**	14.67 \pm 1.23 ^a	6.30 \pm 1.30 ^b	4.10 \pm 0.53 ^b	30.75	<0.001

*Data of leaf area was not normal even after transformation so a Kruskal-Wallis test was used.

**Fresh pod yield was sum of individual fresh weight of bean pods per unit area. The unit was changed to tonnes/ha for better comparison with the literature.

Weed performance under crop monoculture and intercropping conditions

In general, both weed species performed poorly under intercropping (IOB) and onion monoculture (M16O). *C. album* under IOB had significantly lower mean individual aboveground fresh/dry weights than under M16O and M12B (Figure 3, Table 3). *C. album* grown under M16O had the second lowest individual aboveground fresh/dry weights. No significant difference was found between *C. album* grown under M12B and under the control. The same trends were observed in mean individual plant height and leaf area of *C. album* (Table 3).

Mean individual aboveground fresh weights of *A. hybridus* under IOB and M16O were significantly lower than under M12B, which was followed by the control (Figure 4). Mean individual aboveground dry weight of *A. hybridus* also had a similar trend (Table 3). Mean individual height of *A. hybridus* was lowest under IOB, followed by M16O. Plant height of *A. hybridus* under M16B was not significantly different than the control. Similar trend was observed in mean individual leaf area of *A. hybridus* (Table 3).

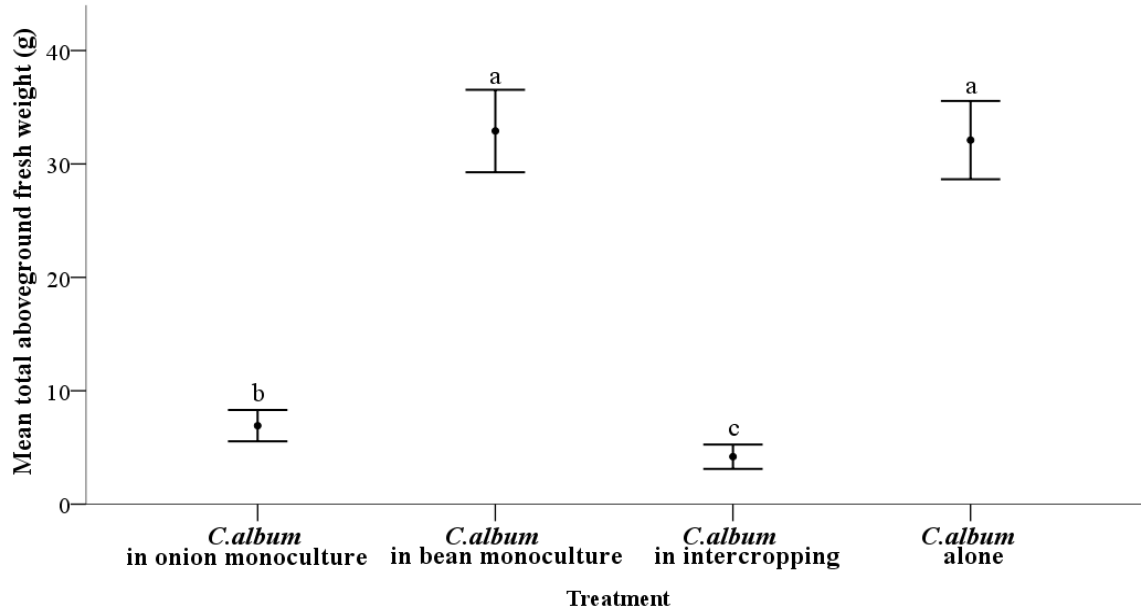


Figure 3. Mean individual total aboveground fresh weight of *C. album* under onion and yellow wax bean monocultures (M16O and M12B), intercropping (IOB) and the control (four weed plants alone). Significance is indicated by letters (a, b, c) above the standard error bars (df=2, MS=10.38, F=128.24, $p<0.001$).

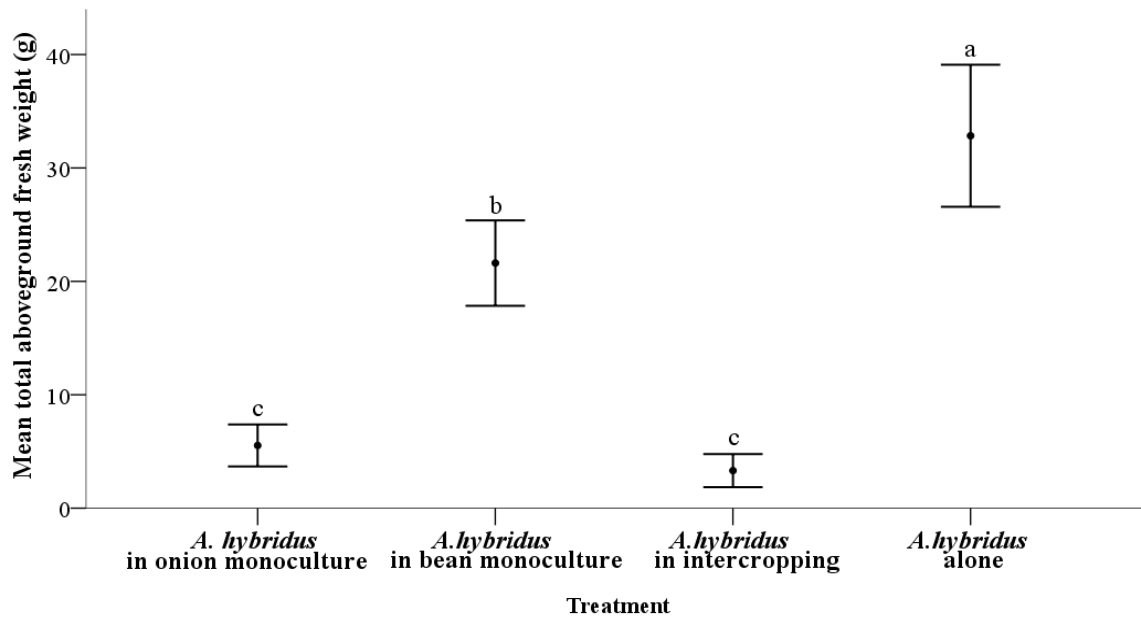


Figure 4. Mean individual total aboveground fresh weight of *A. hybridus* under onion and yellow wax bean monocultures (M16O and M12B), intercropping (IOB) and the control (four weed plants alone). Significance is indicated by letters (a, b, c) above the standard error bars (df=2, MS=5.48, F=51.49, $p<0.001$).

Table 3. Variables measured on *C. album* and *A. hybridus* under onion and yellow wax bean monocultures (M16O and M12B), intercropping (IOB) and the control (four weed plants alone). Significant differences among treatments are indicated by letters in superscript (a, b, c). Mean values (\pm standard error) are the original values without transformation.

Variables	Weeds under onion monoculture (M16O)	Weeds under yellow wax bean monoculture (M12B)	Weeds under intercropping (IOB)	Four weed plants alone (control)	F	P
Individual total aboveground dry weight of <i>C. album</i> (g)	2.10 \pm 0.21 ^b	10.04 \pm 0.59 ^a	1.17 \pm 0.13 ^c	10.31 \pm 0.59 ^a	146.69	<0.001
Individual height of <i>C. album</i> (cm)	54.40 \pm 3.53 ^b	95.72 \pm 3.53 ^a	38.56 \pm 2.71 ^c	98.76 \pm 3.96 ^a	60.01	<0.001
Individual leaf area of <i>C. album</i> (cm ²)	75.45 \pm 4.47 ^b	324.47 \pm 15.69 ^a	40.31 \pm 2.78 ^c	339.36 \pm 19.22 ^a	215.8	<0.001
Individual total aboveground dry weight of <i>A. hybridus</i> (g)	1.47 \pm 0.20 ^b	5.48 \pm 0.52 ^a	0.85 \pm 0.14 ^c	7.55 \pm 0.91 ^a	53.63	<0.001
Individual height of <i>A. hybridus</i> (cm)	25.87 \pm 2.20 ^b	52.63 \pm 2.71 ^a	17.74 \pm 2.05 ^c	50.90 \pm 3.31 ^a	41.46	<0.001
Individual leaf area of <i>A. hybridus</i> (cm ²)	64.50 \pm 8.59 ^c	228.22 \pm 37.64 ^b	12.95 \pm 2.65 ^d	505.71 \pm 32.44 ^a	73.40	<0.001

The performance of *C. album* from six parents from two farms significantly varied under different conditions. When grown under onion monoculture (M16O), mean individual aboveground fresh /dry weights of *C. album* from two populations (farms) were similar, except from CC3 whose weights were significantly greater than those of CO2 (Table 4). Mean plant height of *C. album* was not significantly different between both farms but varied within the conventional farm population (Table 4). Plant height of CC3 was higher than that of CC1 (Table 4). No significant difference was found in mean individual leaf area across plants from different parents under M16O except from plants from CO2, which had significantly lower mean leaf area (Table 4). However, plants from the conventional farm tended to have greater leaf area than plants from the organic farm even though they were not statistically different (Table 4).

No significant differences were observed in measured variables of *C. album* plants from all parents in yellow wax bean monoculture (M12B) (Table A1, see Appendix). Similarly, no significant differences were found in measured variables of *C. album* plants under intercropping (IOB), except from the significantly lower mean individual leaf area of CO1 (Table A2). Under four-weed control, *C. album* plants from CC2 have significantly higher plant height than those from CO1 and CO3 (Table A3). Leaf area of *C. album* plants from CC2 and CC3 was significantly greater than those from the organic farm population (CO1, CO2 and CO3) (Table A3). However, *C. album* plants from different parents in four-weed control did not differ in aboveground fresh /dry weights (Table A3).

There were no significant differences in variables (mean aboveground fresh/dry weight, plant height, leaf area and seeding time) of *A. hybridus* from three parents (PO1, PO2, PO3) from the organic farm population under different conditions (Table A4 - A7).

Table 4. Variables measured on *C. album* plants from different seed parents under onion monoculture (M16O). CC1, CC2, CC3 are plants of three seed parents from the conventional farm, while CO1, CO2, CO3 are plants of three seed parents from the organic farm. Significant differences among treatments are indicated by letters in superscript (a, b, c). Mean values (\pm standard error) are the original values without transformation.

Variables	Conventional farm			Organic farm			F	P
	CC1	CC2	CC3	CO1	CO2	CO3		
Individual aboveground fresh weight (g)	6.30 \pm 1.27 ^{ab}	8.45 \pm 2.29 ^{ab}	11.47 \pm 1.97 ^a	6.84 \pm 1.41 ^{ab}	3.49 \pm 0.60 ^b	7.34 \pm 0.89 ^{ab}	2.98	<0.05
Individual aboveground dry weight (g)	2.08 \pm 0.45 ^{ab}	2.86 \pm 0.96 ^{ab}	2.50 \pm 0.33 ^a	2.11 \pm 0.40 ^{ab}	0.97 \pm 0.19 ^b	2.09 \pm 0.22 ^{ab}	1.60	<0.05
Individual height (cm)	35.98 \pm 6.16 ^b	53.98 \pm 10.10 ^{ab}	80.67 \pm 9.58 ^a	51.68 \pm 6.19 ^{ab}	44.49 \pm 4.35 ^{ab}	59.90 \pm 6.66 ^{ab}	4.24	<0.05
Individual leaf area (cm ²)	90.27 \pm 9.98 ^a	80.96 \pm 11.00 ^a	105.82 \pm 10.60 ^a	76.44 \pm 10.88 ^a	30.71 \pm 3.63 ^b	72.66 \pm 7.35 ^a	8.23	<0.05

Performance of crops with weeds under monoculture and intercropping conditions

The presence of both weed species, *C. album* and *A. hybridus*, significantly reduced onion mean individual total aboveground fresh/dry weights under IOB, but only *A. hybridus* significantly decreased those in M16O (Figure 5, Table 5). Under M16O and IOB, onion weights of fresh leaves and dry bulbs were significantly reduced with the presence of weeds. The presence of weeds did not significantly affect mean individual weights of dry leaves and fresh bulbs and mean individual plant height of onions (Table 5). Fresh bulb yield of onions was also not affected by the presence of weeds both in M16O and IOB (Table 5). Overall, onion grew better in IOB than in M16O regardless of presence or absence of weeds (Figure 5, Table 5).

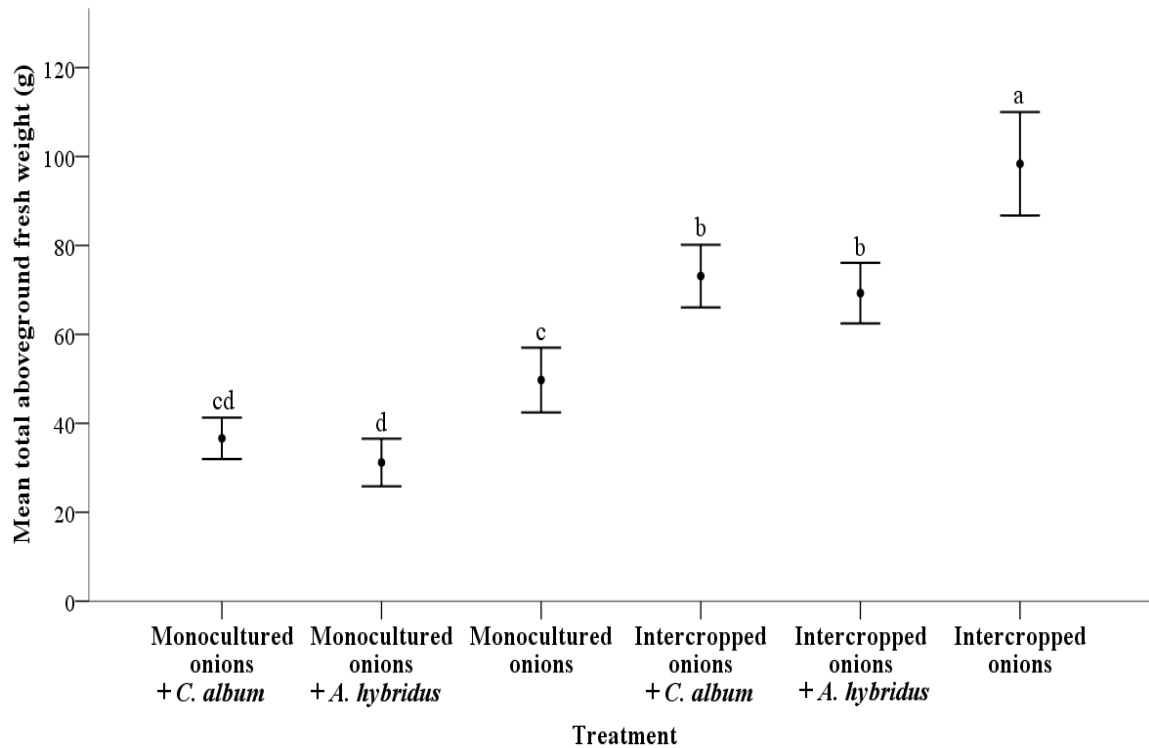


Figure 5. Mean individual total aboveground fresh weight of onions when grown with or without the presence of weeds (either *C. album* or *A. hybridus*) under monoculture (M16O) and intercropping (IOB) conditions. Significance is indicated by letters (a, b, c) above the standard error bars (df=5, MS=17653.76, F=44.23, $p<0.001$).

Table 5. Variables measured on onions when grown with or without the presence of weeds (either *C. album* or *A. hybridus*) under monoculture (M16O) and intercropping (IOB) conditions. Significant differences among treatments are indicated by letters in superscript (a, b, c). Mean values (\pm standard error) are the original values without transformation.

Variables	Monoculture onions with <i>C. album</i>	Monoculture onions with <i>A. hybridus</i>	Monoculture onions without weeds	Intercropped onions with <i>C. album</i>	Intercropped onions with <i>A. hybridus</i>	Intercropped onions without weeds	F	P
Individual total aboveground dry weight (g)	3.85 \pm 0.21 ^{cd}	3.23 \pm 0.27 ^d	4.65 \pm 0.32 ^c	7.49 \pm 0.37 ^b	7.05 \pm 0.37 ^b	9.48 \pm 0.34 ^a	44.10	<0.001
Individual fresh weight of leaves (g)	13.65 \pm 1.56 ^c	10.80 \pm 1.75 ^c	27.65 \pm 2.58 ^b	25.23 \pm 2.39 ^b	19.60 \pm 2.59 ^{bc}	45.05 \pm 4.45 ^a	18.02	<0.001
Individual dry weight of leaves (g)	2.62 \pm 0.19 ^b	2.22 \pm 0.23 ^b	2.42 \pm 0.26 ^b	5.23 \pm 0.31 ^a	5.25 \pm 0.40 ^a	5.58 \pm 0.32 ^a	1.31	<0.001
Individual fresh weight of bulb (g)	22.97 \pm 1.6 ^b	20.37 \pm 1.95 ^b	22.08 \pm 1.70 ^b	47.87 \pm 2.78 ^a	49.67 \pm 3.76 ^a	53.30 \pm 2.61 ^a	31.15	<0.001
Individual dry weight of bulb (g)	1.22 \pm 0.97 ^c	1.00 \pm 0.10 ^c	2.23 \pm 0.12 ^b	2.26 \pm 0.16 ^b	1.79 \pm 0.14 ^b	3.90 \pm 0.85 ^a	34.75	<0.001
Individual height (cm)	49.30 \pm 1.25 ^b	48.86 \pm 1.63 ^b	52.75 \pm 2.08 ^b	61.20 \pm 0.97 ^a	61.97 \pm 1.46 ^a	62.20 \pm 2.46 ^a	19.97	<0.001
Fresh bulb yield (tonnes/hectare)*	40.19 \pm 2.87	37.49 \pm 3.56	38.56 \pm 3.10	41.18 \pm 2.54	43.13 \pm 3.20	46.67 \pm 2.33	0.871	0.502

*Fresh bulb yield was sum of individual fresh bulb weight per unit area. The unit was changed to tonnes/ha for better comparison with the literature.

Generally, yellow wax bean performed poorly when weeds were present: the presence of weeds significantly reduced mean individual total aboveground fresh/dry weights of yellow wax bean in the bean monoculture (M12B) but only *C. album* reduced those in intercropping (IOB) (Figure 6, Table 6). The same trends were observed in mean individual fresh/dry shoot (leaves and stems) weights and individual fresh pod weights (Table 6). The presence of weeds significantly decreased mean individual dry pod weight in M12B but had no significant effects on the bean in IOB (Table 6).

Presence of weeds significantly reduced mean individual plant height of yellow wax beans in M12B but had no effects on that of the bean in IOB (Table 6). However, mean individual leaf area of yellow wax beans was significantly decreased by the presence of weeds in both monoculture and intercropping conditions. *C. album* reduced leaf area of the bean in IOB more than *A. hybridus* did (Table 6). The fresh pod yield (sum fresh pod weight per pot) in M12B was significantly reduced by the presence of weeds but it was not affected by weeds under IOB (Table 6).

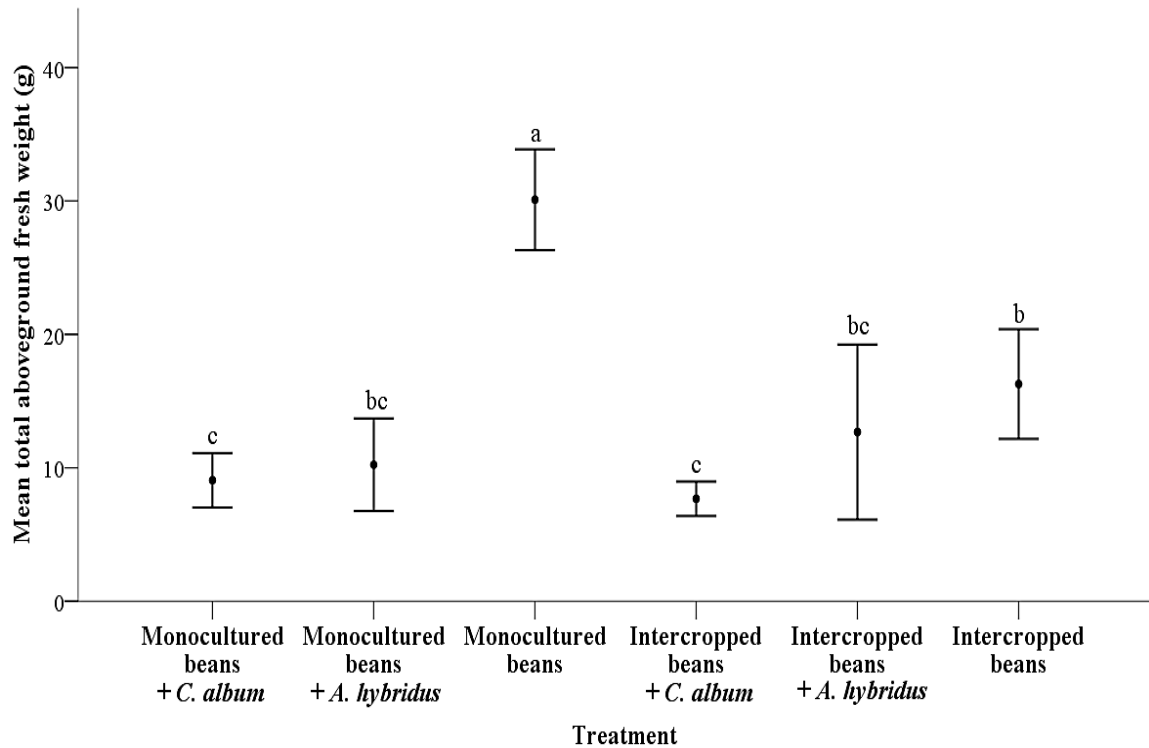


Figure 6. Mean individual total aboveground fresh weight of yellow wax beans when grown with or without the presence of weeds (either *C. album* or *A. hybridus*) under monoculture (M12B) and intercropping (IOB) conditions. Significance is indicated by letters (a, b, c) above the standard error bars (df=5, MS=1.23, F=13.82, $p < 0.001$).

Table 6. Variables measured on yellow wax beans when grown with or without the presence of weeds (either *C. album* or *A. hybridus*) under monoculture (M12B) and intercropping (IOB) conditions. Significant differences among treatments using are indicated by letters in superscript (a, b, c). Mean values (\pm standard error) are the original values without transformation.

Variables	Monoculture beans with <i>C. album</i>	Monoculture beans with <i>A. hybridus</i>	Monoculture beans without weeds	Intercropped beans with <i>C. album</i>	Intercropped beans with <i>A. hybridus</i>	Intercropped beans without weeds	F	P
Individual total aboveground dry weight (g)	1.04 \pm 0.10 ^c	1.15 \pm 0.19 ^{bc}	3.30 \pm 0.18 ^a	0.86 \pm 0.06 ^c	1.25 \pm 0.26 ^{bc}	1.69 \pm 0.21 ^b	18.18	<0.001
Individual fresh weight of shoots (g)	5.84 \pm 0.64 ^{bc}	6.44 \pm 1.08 ^{bc}	18.08 \pm 1.02 ^a	4.56 \pm 0.43 ^c	7.64 \pm 1.98 ^{bc}	9.97 \pm 1.16 ^b	14.04	<0.001
Individual dry weight of shoots (g)	0.75 \pm 0.08 ^c	0.85 \pm 0.14 ^{bc}	2.40 \pm 0.4 ^a	0.62 \pm 0.56 ^c	0.76 \pm 0.13 ^{bc}	1.19 \pm 0.13 ^b	16.20	<0.001
Individual fresh weight of pods (g)	3.23 \pm 0.39 ^c	3.79 \pm 0.67 ^{bc}	12.02 \pm 0.96 ^a	3.11 \pm 0.26 ^c	5.03 \pm 1.38 ^{bc}	6.30 \pm 0.94 ^b	10.91	<0.001
Individual dry weight of pods (g)	0.30 \pm 0.04 ^b	0.30 \pm 0.06 ^b	0.90 \pm 0.07 ^a	0.24 \pm 0.02 ^b	0.49 \pm 0.14 ^b	0.50 \pm 0.11 ^b	13.26	<0.001
Individual height (cm)	22.95 \pm 0.93 ^b	23.71 \pm 1.80 ^b	33.50 \pm 0.76 ^a	20.66 \pm 0.71 ^b	24.06 \pm 1.26 ^b	25.90 \pm 1.81 ^b	6.63	<0.001
Individual leaf area (cm ²)	117.18 \pm 7.66 ^c	139.63 \pm 9.65 ^c	494.38 \pm 16.85 ^a	44.86 \pm 3.97 ^d	98.40 \pm 9.60 ^c	292.09 \pm 20.53 ^b	12.18	<0.001
Fresh pod yield (tonnes/hectare)*	3.47 \pm 0.43 ^b	4.27 \pm 0.73 ^b	14.67 \pm 1.23 ^a	2.10 \pm 0.17 ^b	3.23 \pm 0.87 ^b	4.10 \pm 0.53 ^b	35.32	<0.001

*Fresh pod yield was sum of individual fresh weight of bean pods per unit area. Unit was changed to tonnes/ha for better comparison with the literature.

Phenotypic differences of C. album from the conventional and organic farms

When grown under “one plant per pot condition” (no competition), individual aboveground fresh/dry weights of *C. album* plants from different parents were not different from each other except for CC1. Plants from CC1 had significantly higher mean individual aboveground fresh/ dry weights than the others (Table 7). *C. album* from the conventional farm population had significantly greater plant height than those from the organic farm except for CC3, which was similar to CO1 (Table 7). Plants from CC3 and CO1 were intermediate between the other individuals coming from organic and conventional farms. Mean individual leaf area of *C. album* from the conventional farm was significantly greater than that of those from the organic farm (Table 7). It was observed that *C. album* from the organic farm population had earlier seeding time (about 17 days) and more seeds (seed number was not counted, personal observation) than those from the conventional farm.

Table 7. Variables measured on *C. album* plants under the “one plant per pot” condition. CC1, CC2, CC3 are plants of three seed parents from the conventional farm, while CO1, CO2, CO3 are plants of three seed parents from the organic farm. Significant differences are indicated by letters in superscript (a, b, c). Mean values (\pm standard error) are the original values without transformation.

Variables	Conventional farm			Organic farm			F	P
	CC1	CC2	CC3	CO1	CO2	CO3		
Individual aboveground fresh weight (g)	18.83 \pm 1.23 ^a	12.32 \pm 0.50 ^b	13.14 \pm 1.03 ^b	13.31 \pm 0.92 ^b	11.10 \pm 0.39 ^b	12.77 \pm 1.26 ^b	8.02	<0.001
Individual aboveground dry weight (g)	5.74 \pm 0.40 ^a	3.61 \pm 0.18 ^b	3.94 \pm 0.29 ^b	3.78 \pm 0.32 ^b	3.36 \pm 0.18 ^b	4.01 \pm 0.41 ^b	7.43	<0.001
Individual height (cm)	92.18 \pm 3.05 ^a	78.26 \pm 1.86 ^b	64.51 \pm 5.77 ^{bc}	66.99 \pm 5.54 ^{bc}	54.25 \pm 1.57 ^c	53.99 \pm 1.93 ^c	15.76	<0.001
Individual leaf area (cm ²)	228.65 \pm 12.39 ^a	211.50 \pm 9.09 ^a	176.29 \pm 12.75 ^a	108.89 \pm 14.89 ^b	95.86 \pm 5.93 ^b	105.06 \pm 17.22 ^b	21.65	<0.001

Discussion

Growth of onion and yellow wax bean under intercropping vs. monocultures

The first objective of this study was to investigate the effects of interactions between onion and yellow wax bean when grown under monoculture (intraspecific interactions) as well as intercropping (intraspecific and interspecific interactions) conditions. The results showed that onion grew better when intercropped with yellow wax bean (IOB) than in onion monocultures (both M16O and M8O). However, the growth of yellow wax bean under IOB was reduced when compared to bean monocultures (both M12B and M6B). In addition, the RYT value was 1.3, indicating that the IOB had yield advantages than both M16O and M12B. Tofinga (1993) suggested that if a RYT value is higher than 1.0, it indicates that at least one crop grows better in intercropping than in monoculture. The occurrence of resource partitioning can result in a RYT value that ranges from 1.0 to 2.0 (Tofinga 1993, Sobkowicz and Podgórska-Lesiak, 2007; Eskandari, 2011). The RII value of onion was 0.35. This showed that a mild facilitative effect on onion would be found with the presence of yellow wax bean. On the other hand, yellow wax bean had a RII value of -0.21, suggesting a mild competitive effect against yellow wax bean in the presence of onion (Armas *et al.*, 2004).

The growth and yield of crops under intercropping are influenced by complex plant interactions (Malézieux *et al.*, 2009). The asymmetric benefit of two crops in intercropping has been observed in previous studies (Zhang and Li, 2003; Eskandari, 2011). It is found that the better growth of crops in intercropping than in monocultures is associated with reduced competition due to resource partitioning (Malézieux *et al.*, 2009; Lithourgidis *et al.*, 2011). Resource partitioning can occur if two intercropped species

have different leaf and root morphologies, plant heights, root depths or soil nutrient uptake rates and requirements (Postma and Lynch, 2012; Belel *et al.*, 2014). These allow two intercropped species to exploit sunlight, water, soil space and nutrients in different manners, minimizing competition (Belel *et al.*, 2014). The reduced competitive effects can lead to the better growth of crops than in their monocultures (Malézieux *et al.*, 2009). Cereal-legume intercropping systems have used two crop species with different root morphologies and depths, minimizing belowground competition for soil space and leading to the better growth of the cereals than in cereal monocultures (Belel *et al.*, 2014). Similarly, when wheat is intercropped with faba bean, the two species uptake soil nutrients at different rates, leading to the better growth of wheat than in monoculture (Eskandari, 2011). Previous studies found that onion and yellow wax bean have different root depths and architectures (Weaver and Bruner, 1927) as well as different requirements for soil N and P (Graham *et al.*, 1997; Coolong *et al.*, 2004; Rizk *et al.*, 2012). Resource partitioning might occur between these two crops and might lead to reduced competition. If the competitive effects of yellow wax bean against onion are less than the intraspecific competition against onion itself, onion under the IOB is expected to acquire more soil space and resources than onion under the M16O. This might be associated with the better growth of onion under the IOB when compared to the M16O.

The better growth of one crop than another is affected by the competitiveness of crop species in the mixture (Zhang and Li, 2003). Aboveground competition of crops is influenced by plant height and canopy structures (Addo-Quaye *et al.*, 2011). Crops with lower ability in capturing sunlight are usually planted before those with higher in order to balance the competitive ability of crops in the mixture (Addo-Quaye *et al.*, 2011, Belel *et*

al., 2014). Studies suggested that onion is a weak competitor for sunlight when compared to yellow wax bean because bean has greater leaf surface than onion (Patel *et al.*, 2012; Stagnari and Pisante, 2011). In my experiment, yellow wax bean was planted 20 days after emergence of onions in the IOB, intending to reduce the aboveground competition of yellow wax bean against onion. However, even though this might be able to balance the aboveground competition between onion and yellow wax bean, it might also affect the belowground competition between the two species.

Studies found that belowground competition may be as important, if not more, in affecting plant growth as aboveground competition (Aspasia *et al.*, 2009; DeHaan and Vasseur, 2014). Dunbabin (2007) suggested that effective occupation of soil volume by roots makes plants prevail in belowground competition. Since onion was planted before yellow wax bean, the root occupancy of onion might have denied the establishment of the bean's root systems. The lower growth of yellow wax bean under IOB than might be associated with a poorly extended root system which constrains the bean to effectively uptake soil water and nutrients (Aspasia *et al.*, 2009). In addition, a previous study found that interspecific competition for soil nutrients can also result in better growth and yield of the species that have higher nutrient uptake rate but suppress those species that have less (Zhang and Li, 2003). This phenomenon is also reported when wheat grown with maize or wheat grown with soybean where wheat is more aggressive in acquiring N, P and K than the other two crops and became dominant (Lithourgidis *et al.*, 2011). The poor growth of yellow wax bean and better growth of onion under IOB might be associated with their different nutrient uptake rates and might indicate that onion was more aggressive in soil nutrient uptake.

Interactions in intercropped species may also originate from the production of complex allelochemicals, which can promote or suppress the growth of plants and thus affect crop yield (Lithourgidis *et al.*, 2011; Farooq *et al.*, 2011). Facilitative effects in intercropping can be due to nutrient enrichment by component crops (Farooq *et al.*, 2011). Studies found that legumes can excrete protons, carboxylates and phosphatases into their rhizosphere to mobilize soil P from insoluble to soluble forms (Maingi *et al.*, 2001; Hinsinger *et al.*, 2011). *P. vulgaris* has been shown to increase soil P availability, benefiting its intercropped neighbors (Graham and Ranalli, 1997; Kouas *et al.*, 2009). For example, in common bean (*P. vulgaris*)-durum wheat intercropping both shoot and root masses of durum wheat increase, probably due to an increase in soil inorganic P associated with the root excretion of *P. vulgaris* (Li *et al.*, 2008). In addition, facilitation may also be related to growth promoting compounds such as plant hormones or other allelochemicals, which can affect the physiological process (i.e. nutrient uptake rate) of other plant species (Amin *et al.*, 2007). While one may hypothesize that these effects are associated with the better growth of onion under IOB, further studies on soil P content, the nutrient uptake rate of both crops under mixture vs. their monocultures and the analysis of potential allelochemicals will be required.

Similarly, the reduced growth of yellow wax bean under IOB when compared to M12B and M6B might be related to negative allelopathic effects of onion. However, if allelopathy occurred, the results are not consistent with what has been reported in previous studies, in which onion has shown potentially positive allelopathic effects on cucumber (*Cucumis sativus* L.) and on lettuce, promoting the growth of these two crop species (Zhou *et al.*, 2011; DeHaan and Vasseur, 2014). However, a study suggested that

the effects of allelochemicals on plants are species-specific (Kruidhof *et al.*, 2008). That means the same compounds that can promote growth of one species may inhibit growth of another (Kruidhof *et al.*, 2008). Further studies can focus on the effects of aqueous extracts from onion roots, bulbs and leaves on the growth of yellow wax bean and other crop species to find out the potential allelopathic compounds.

Effects of plant density on crop performance in monocultures

Under monoculture (M16O vs. M8O; M12B vs. M6B), yield and individual total aboveground dry weight of both crops did not vary under two planting densities. In most cases, at sufficiently high planting densities, individual plant growth (dry mass per plant) is constrained by competition for space and resources (Weiner and Freckleton, 2010). However, this was not observed in the study. One possible explanation is that both planting densities were not high enough to limit plant dry weight accumulation, indicating that sufficient space and resources for both crops might exist and intraspecific competition may be too low to constrain plant total aboveground dry weight (Paiva *et al.*, 2014). However, even though two crops did not differ in yield and individual total aboveground dry weight under two planting densities, individual total aboveground fresh weight of two crops was higher under the higher density. This means that two crops under the higher density had higher water content. Taheri Asghari (2009) found that plants under high densities will increase root diameter and water absorption rate probably due to a response in soil moisture fluctuations. Further investigation on how root morphologies and plant water contents vary under different soil moisture levels can provide more information to explain the inconsistency of individual total aboveground fresh vs. dry weights of onion and yellow wax bean under two planting densities.

The result also found that individual onion plants had higher dry bulb weight while individuals of yellow wax bean had greater plant height, shoot mass and leaf area when exposed to the higher density. The higher dry bulb weight of onion in M16O than in M8O remains difficult to explain. For yellow wax bean, these weight and morphology variations in different aboveground parts might be associated with the response to sunlight fluctuations (Aerts *et al.*, 1991; Xiao *et al.*, 2006). A previous study found that under different planting densities, light levels fluctuate due to different shading patterns (Xiao *et al.*, 2006). Plants are able to alter height, leaf area per unit, leaf mass and stem mass in response to different sunlight conditions (Corré, 1983; Schmitt *et al.*, 1999; Xiao *et al.*, 2006). While light levels were not quantified in this study, this speculation can be further studied by investigating how onion and yellow wax bean will respond to different light intensities.

Crop-weed performance in monoculture

The second objective of this study was to investigate the growth of crops and weeds under crop monoculture and intercropping conditions. The results found that weed total aboveground fresh/dry weights were reduced around five times under onion monoculture (M16O). On the other hand, the presence of weeds reduced individual total aboveground fresh/dry weights of onion by approximately 30%.

Onion fields are well known to suffer weed infestation due to the crop's characteristics such as slow initial growth rate, non-branching growth habit, cylindrical upright leaves and shallow fibrous roots (Porwal and Singh, 1993; Gazdag-Torma, 1997; Mennan and Isik, 2003; Patel *et al.*, 2012). Studies found that direct-seeded onions have to be kept weed free for 40-56 days after emergence to prevent yield loss (Gazdag-Torma,

1997; Patel *et al.*, 2012). In my experiment, since onions were kept weed free for only 25 days (weeds usually emerge when onion is growing), it is not surprising that the growth of onion was reduced by the presence of weeds. However, the growth of two weeds was reduced more than the growth of onion in the M16O when compared to the four-weed control. It is mentioned in the previous section that timing of the emergence of plant species can have an impact on the balance of resource competition (Dunbabin, 2007). This is also reported in crop-weed competition studies (Dunbabin, 2007; Tironi *et al.*, 2014). The physical occupation of soil space by the established crop roots may deny weeds from further occupation (Dunbabin, 2007). In my study, this might be able to explain why weed growth was reduced more than onion's growth when compared to the controls.

In addition, it is found that spatial arrangement of crops can affect the growth of crops and weeds (Marín and Weiner, 2014). Olsen *et al* (2005) found that a uniformly spatial arrangement with a proper planting density can reduce weed intrusion. This is because spatial uniformity can reduce intraspecific competition between crop individuals by better and fully utilizing the physical space and resources and leaves fewer resources available for weeds (Olsen *et al.*, 2005; Marín and Weiner, 2014). This occurs especially when weeds emerge after the crop's initial growth stage (Olsen *et al.*, 2006). In my study, onion seeds in the experiment were sown in a uniform pattern. This spatial arrangement plus the earlier root occupancy of the soil volume might be both related to the reduced weed growth in M16O.

The results found that the growth variables of *C. album* and *A. hybridus* under yellow wax bean monoculture were not reduced while the growth of yellow wax bean in

monoculture was reduced by the presence of both weed species. Studies have reported yield loss in *P. vulgaris* fields due to weed infestation (Malik *et al.*, 1993; Aguyoh and Masiunas, 2003; Dusabumuremyi *et al.*, 2014). It is found that bean (*P. vulgaris*) must be kept weed-free for 11-29 days to allow leaf area to fully develop so that it can overshadow weeds and prevent yield loss (Stagnari and Pisante, 2011). This is because the competitiveness of legumes results from the high overall leaf area and planophile leaves that allow them to prevail in sunlight competition (Bilalis *et al.*, 2010). This also means that legumes may not have competitive advantages against weeds if they have not developed a sufficient canopy (Flores-Sanchez *et al.*, 2013; Hayden *et al.*, 2014). In my experiment, weeds emerged 5 days after the germination of yellow wax bean which might not give enough time for the bean to establish a sufficient leaf area. Especially the two studied weed species have reported a fast growth rate and they can enhance stem elongation rapidly in response to sunlight competition (Mahoney and Swanton, 2008). These may explain the reduced growth of yellow wax bean when two weeds were present.

Both weed species in this study have reported allelopathic potential to crops (Alam *et al.*, 2002; Hakimi Rezaei, 2013). Aqueous leaf extracts of *C. album* can reduce shoot height, root length and dry weight of wheat seedlings (Alam *et al.*, 2002). Root and leaf extracts of *C. album* decreased the germination rate and growth of soybean (Alam *et al.*, 2002; Namvar *et al.*, 2009). Similarly, *A. hybridus* has negative effects on germination and growth of several crop species potentially due to allelochemicals (Hakimi Rezaei, 2013). Negative allelopathic effects of weeds might have also played a role in the outcomes of this experiment. This suggests that further study on the allelopathic effects of two weed species on onion and yellow wax bean would be required.

Crop-weed performance in intercropping

The results found that the growth of two weed species (individual total aboveground fresh/dry weight and plant height) was lower in intercropping than in monocultures of both onion and yellow wax bean. On the other hand, crop yield in intercropping was less reduced than that in monoculture with the presence of weeds. These results are consistent with many other intercropping studies, suggesting that crop diversification helps reduce weed problems and stabilize crop yield (Bilalis *et al.*, 2010; Lithourgidis *et al.*, 2011; Corre-Hellou *et al.*, 2011). The assumption is that by having a greater diversity of crops, different plant architectural structures are present, reducing the ability of weeds to suppress crop growth (Belel *et al.*, 2014). To explain these outcomes, ecologists have introduced two hypotheses: the “sampling effect hypothesis” and the “complementarity hypothesis” (Huston, 1997; Tilman, 1997). The “sampling effect hypothesis” says that intercropping systems are more likely to contain highly competitive crop species against weeds (Dukes, 2002). The “complementarity hypothesis” says that intercropping systems are more likely to contain species that acquire resources at different time and spatial scale, utilizing resources more completely and leaving less for weeds (Fargione and Tilman, 2005). However, empirical evidence for these two hypotheses remains rare (Frankow-Lindberg *et al.*, 2009).

Fargione and Tilman (2005) found that monoculture of *S. scoparium* reduced weed growth better than any other 18 monocultures. In addition, intercropping reduced weed growth better than *S. scoparium* monoculture. This suggested that both “sampling” and “complementarity” effects can contribute to weed resistance. Studies found that proper selection of compatible crop species may allow a more complete use of both

above- and belowground space and resources, leading to the a lower weed invasion potential (Malézieux *et al.*, 2009; Belel *et al.*, 2014). This may explain my finding that intercropping onion with yellow wax bean reduced weed growth more than the respective monocultures. My observations showed that most individual weeds appeared etiolated in intercropping (results not shown) and this might suggest that weeds have experienced deficiency of sunlight and soil resources. In the intercropping, the earlier emergence of onion might deny weeds from acquiring belowground soil space and resources. Then the fast development of yellow wax bean canopy might deny weeds from sufficient sunlight and inhibit weed growth. The presence of onion in intercropping is important to resist weed growth as can be seen from the results in onion monoculture with weeds. However, the role of the component species (yellow wax bean) is also crucial in intercropping as it might be associated with the “complementarity effect”. Further studies can investigate if diverse plots can explore both sunlight and soil resources better than monoculture plots in order to better understand how “sampling” and “complementarity” effects can contribute to weed invasion.

Phenotypic variation of C. album from the conventional and organic farms

Results of the common garden experiment showed that the conventional farm population had generally greater individual height and leaf area and slower seeding time than plants from the organic farm. However, individual fresh/dry weights of *C.album* did not significantly differ between both farms. Since the plants were grown under controlled and constant conditions, these observed morphological differences are likely to be the indication of potential local adaptation although maternal effect can still be present (Bommarco *et al.*, 2010). Investment in vegetative growth such as the increase in shoot

mass and height of weeds is usually related to the competitive ability for sunlight (Weinig, 2005; Bommarco *et al.*, 2010). Weed populations that experienced continuous competition with crop species that have strong sunlight capturing ability may develop greater leaf area and height (Murphy and Lemerle, 2006). This is because long term competition against a single crop species or a single crop community favours weed traits that help the weed to prevail in a competitive environment (Murphy and Lemerle, 2006). For example, using a common garden experiment, Weinig (2000) also shows that agricultural weed *Abutilon theophrasti* from different cropping fields (maize or soybean) exhibit differences in elongation time due to long term competition with these different crop species. In my study, the differences in leaf area and height of *C. album* plants from two farms might be associated with a long term competition with crop species that have been cultivated on the farms. However, one should be aware that having smaller leaf area and shorter are not necessary to be less competitive. For example, *C. album* plants from the organic farm had smaller leaf area but similar individual dry weight when compared to those from the conventional farm. This may indicate a different photosynthetic efficiency of *C. album* plants between two populations.

Selective pressures on farms not only depend on the types of crop but also the continuous application of agrochemicals (Gazdag-Torma 1997; Murphy and Lemerle, 2006). Increase in soil nutrients through fertilizers may change the outcomes of crop-weed competition (Guglielmini *et al.*, 2000; Murphy and Lemerle, 2006). Differential N uptake by plants can contribute to variations in plant size for both weeds and crops and may have an impact on their competitive advantages (Guglielmini *et al.*, 2000). The application of chemical fertilizers can increase the growth rate and plant size of crops

(Murphy and Lemerle, 2006). Weeds in such an environment therefore, have to grow faster, taller and produce more leaf area to survive the competition against these crops (Murphy and Lemerle, 2006). This means chemical fertilizers indirectly select weed traits that can prevail in the competition (Murphy and Lemerle, 2006). This may explain the greater leaf area and plant height of *C. album* plants from the conventional farm since chemical fertilizers are used in the farm.

The slower seeding time of *C. album* from the conventional farm might be a trade-off between the investment in reproduction and vegetative growth (Bommarco *et al.*, 2010). Plants that allocate more resources in shoot and leaves will compensate by having later flowering and seed production (Bommarco *et al.*, 2010). Seeding time of weeds can also be an adaptation to water and harvesting regimes because these disturbances are associated with the success of weed seed dispersal (Murphy and Lemerle, 2006).

Adaptive traits in weeds are not caused by a single selective pressure but a combination of these factors (Bommarco *et al.*, 2010). Cropping systems are based on various complex agricultural practices including crop rotation regimes, fertilizer applications and different harvest, tillage and irrigation methods. All of those practices may have influence on weed growth and crop-weed competition (Bommarco *et al.*, 2010). To understand how farming practices can cause evolutionary responses in weeds, further research on weed demography and population dynamics at farms that have a clear disturbance regime will be required.

Implications of this study for vegetable production and weed management

Increasing global population becomes a threat to food security and environmental sustainability. Modern monoculture has shown its limitation to meet the needs of

sustainable development due to the use of agrochemicals and environmental contamination (Malézieux *et al.*, 2009). Intercropping provides an alternative way by using plant-plant interactions to maintain food production without the use of harmful chemicals (Lithourgidis *et al.*, 2011; Belel *et al.*, 2014). In successful intercropping, growth and yield of component crops are promoted due to reduced competition and positive interactions (Liebman and Dyck, 1993). However, the combination of crops and the agronomic management have to be carefully considered (Belel *et al.*, 2014). In this study, intercropping of onion and yellow wax bean was not an ideal system for farmers since only onion had an increase in yield. However, in an ecological perspective, the unknown mechanisms in this system are worth further investigation. For example, it would be useful to know how the timing of planting, plant density and belowground interactions may have affected the growth of both crops in intercropping. Better understanding of plant interactions is crucial to the development and management of agricultural systems, especially for the current greenhouse cultivations industry.

Greenhouse agricultural industry is becoming increasingly popular all over the world. According to the Ontario Ministry of Agriculture (www.omafra.gov.on.ca), from 2008 to 2013, total greenhouse area in Canada increased by approximately 20% and the total value of greenhouse vegetables increased from \$0.9 billion to \$1.2 billion during this period. Better understanding of plant-plant interactions could potentially save greenhouse space, enhance yield and profit and reduce herbicide use. For example, proper selection of two or more crop species based on their leaf morphologies with a proper spatial arrangement might enable the full use of greenhouse space and increase crop production per unit area. The greenhouse industry faces various challenges related to

the current practices including application of high concentrations of nutrients and other chemicals which can cause soil and water pollution through leaching. Better use of facilitative interactions between intercrop species can also potentially reduce the use of chemicals.

In addition, the results of this study might also suggest some ways for sustainable weed control. The growth of weeds was reduced under onion monoculture and this is probably associated with the agronomic manipulations such as time of planting, crop density and planting pattern. Proper agronomic management can increase the competitiveness of crops against weeds (Aspasia *et al.*, 2009). Maximizing the weed-free period and using a proper planting pattern could reduce weed incidences and yield loss (Dunbabin, 2007). Secondly, this study found that intercropping reduced weed growth and stabilized crop yield better than monoculture as has been reported in other studies (Lithourgidis *et al.*, 2011; Corre-Hellou *et al.*, 2011). With the proper selection of crop species in intercropping, it is possible to optimize resource use and minimize weed intrusion (Belel *et al.*, 2014). Weed management through crop mixture meets the needs of sustainable agriculture as it maintains ecological functions of crop diversity and meanwhile reduces the use of herbicides (Lithourgidis *et al.*, 2011). Especially today, long term herbicide usage has been shown to cause resistance of many weed species, making chemical control a great challenge.

General conclusion

In agricultural settings, like any other plant communities, interactions are complex. Competitive and facilitative interactions in agricultural fields can affect the growth, survival, production of individual plants and the coexistence or exclusion of plant species. Intercropping onion with yellow wax bean showed facilitative effects on onion growth but reduced the growth of yellow wax bean. A better understanding of the mechanisms behind the increased growth of onion may help define new methods to increase crop production with reduced or without use of fertilizers.

The study supports the argument that intercropping reduces weed infestation better than monocultures. Two hypotheses in invasion ecology, the “sampling” and “complementarity” effects may explain this result. Further investigation of the mechanisms behind both hypotheses may not only help better control agricultural weeds but may also provide an insight in controlling invasive plant species in other ecosystems through the use of functional groups.

Selective pressures on weeds make the prediction of the direction of the shift in weed populations difficult. Variation in morphological traits between weed populations in different farms may be an indicator for different selective pressures. When herbicide resistances are reported for weeds, one should be aware that these selective pressures can also make weeds adapt and become harder to control.

The limitation of this study is that belowground interactions between plants were not well investigated due to logistical issues in the greenhouse. The growth of plants in this study was likely affected by complex belowground interactions such as nutrient competition, enrichment and allelopathy. In sum, crop diversification should continue to

be considered as an alternative for optimizing crop production and as a weed control method. Better understanding plant interactions in further studies could benefit the design and management of intercropping systems.

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Appendix

Table A1. Variables measured on *C. album* plants from different seed parents under yellow wax bean monoculture (M12B). CC1, CC2, CC3 are plants of three seed parents from the conventional farm, while CO1, CO2, CO3 are plants of three seed parents from the organic farm. Mean values (\pm standard error) are the original values without transformation.

Variables	Conventional farm			Organic farm			F	P
	CC1	CC2	CC3	CO1	CO2	CO3		
Individual aboveground fresh weight (g)	31.76 \pm 3.13	37.45 \pm 3.32	37.99 \pm 3.93	32.35 \pm 6.98	24.13 \pm 3.35	35.10 \pm 4.39	0.21	0.96
Individual aboveground dry weight (g)	9.97 \pm 1.15	11.27 \pm 1.05	11.16 \pm 1.48	10.59 \pm 2.31	6.74 \pm 0.78	10.32 \pm 1.22	1.31	0.28
Individual height (cm)	99.95 \pm 10.00	94.41 \pm 6.53	99.53 \pm 7.94	98.53 \pm 12.73	91.22 \pm 8.82	91.31 \pm 7.57	1.34	0.27
Individual leaf area (cm ²)	375.78 \pm 39.32	358.74 \pm 42.84	256.47 \pm 32.85	254.97 \pm 47.32	291.01 \pm 38.44	302.72 \pm 59.75	1.74	0.13

Table A2. Variables measured on *C. album* plants from different seed parents under intercropping (IOB). CC1, CC2, CC3 are plants of three seed parents from the conventional farm, while CO1, CO2, CO3 are plants of three seed parents from the organic farm. Significant differences among treatments are indicated by letters in superscript (a, b, c). Mean values (\pm standard error) are the original values without transformation.

Variables	Conventional farm			Organic farm			F	P
	CC1	CC2	CC3	CO1	CO2	CO3		
Individual aboveground fresh weight (g)	3.97 \pm 1.81	5.40 \pm 1.07	5.73 \pm 0.99	2.90 \pm 0.74	5.89 \pm 1.92	3.57 \pm 0.55	1.59	0.18
Individual aboveground dry weight (g)	1.13 \pm 0.53	1.29 \pm 0.27	1.42 \pm 0.19	0.85 \pm 0.24	1.39 \pm 0.42	0.97 \pm 0.15	1.52	0.20
Individual height (cm)	30.28 \pm 8.48	34.61 \pm 4.87	51.97 \pm 8.52	31.61 \pm 3.37	44.15 \pm 7.63	39.48 \pm 3.30	1.09	0.38
Individual leaf area (cm ²)	35.58 \pm 6.31 ^{ab}	62.67 \pm 9.41 ^a	51.27 \pm 6.41 ^a	24.13 \pm 2.95 ^b	40.35 \pm 4.23 ^a	43.51 \pm 6.57 ^{ab}	4.42	< 0.05

Table A3. Variables measured on *C. album* plants from different seed parents under the four-weed control. CC1, CC2, CC3 are plants of three seed parents from the conventional farm, while CO1, CO2, CO3 are plants of three seed parents from the organic farm. Significant differences among treatments are indicated by letters in superscript (a, b, c). Mean values (\pm standard error) are the original values without transformation.

Variables	Conventional farm			Organic farm			F	P
	CC1	CC2	CC3	CO1	CO2	CO3		
Individual aboveground fresh weight (g)	27.90 \pm 3.02	40.45 \pm 4.03	36.82 \pm 4.50	32.59 \pm 3.32	27.58 \pm 4.28	29.65 \pm 3.05	1.92	0.16
Individual aboveground dry weight (g)	9.26 \pm 1.01	12.41 \pm 1.79	11.12 \pm 1.37	11.51 \pm 1.49	7.53 \pm 2.52	9.98 \pm 1.30	1.80	0.18
Individual height (cm)	102.61 \pm 8.17 ^{ac}	117.28 \pm 2.83 ^a	114.68 \pm 4.37 ^{ab}	86.50 \pm 8.02 ^{bc}	88.35 \pm 8.96 ^{ac}	83.13 \pm 2.45 ^c	5.55	<0.05
Individual leaf area (cm ²)	300.9 \pm 16.79 ^c	404.3 \pm 46.14 ^b	560.9 \pm 42.38 ^a	279.5 \pm 29.11 ^{bc}	235.2 \pm 23.39 ^c	259.4 \pm 10.01 ^c	16.08	<0.001

Table A4. Variables measured on *A. hybridus* plants from different seed parents under onion monoculture (M16O). PO1, PO2, PO3 represent plants of three seed parents from the organic farm. Mean values (\pm standard error) are the original values without transformation.

Variables	PO1	PO2	PO3	F	P
Individual aboveground fresh weight (g)	5.02 \pm 3.20	6.91 \pm 2.07	5.84 \pm 1.71	0.34	0.74
Individual aboveground dry weight (g)	1.40 \pm 0.22	1.76 \pm 0.46	1.27 \pm 0.30	0.60	0.55
Individual height (cm)	25.52 \pm 3.93	27.82 \pm 3.76	24.11 \pm 4.12	0.25	0.81
Individual leaf area (cm ²)	70.69 \pm 8.65	56.22 \pm 9.70	66.60 \pm 7.14	0.80	0.45

Table A5. Variables measured on *A. hybridus* plants from different seed parents under yellow wax bean monoculture (M12B). PO1, PO2, PO3 represent plants of three seed parents from the organic farm. Mean values (\pm standard error) are the original values without transformation.

Variables	PO1	PO2	PO3	F	P
Individual aboveground fresh weight (g)	24.24 \pm 2.94	24.14 \pm 4.13	23.21 \pm 2.24	0.32	0.97
Individual aboveground dry weight (g)	4.48 \pm 0.43	6.40 \pm 1.26	5.28 \pm 0.44	0.50	0.61
Individual height (cm)	50.93 \pm 3.84	58.94 \pm 4.29	48.03 \pm 5.61	1.54	0.24
Individual leaf area (cm ²)	276.85 \pm 65.34	189.47 \pm 73.48	144.76 \pm 59.10	0.58	0.57

Table A6. Variables measured on *A. hybridus* plants from different seed parents under intercropping (IOB). PO1, PO2, PO3 represent plants of three seed parents from the organic farm. Mean values (\pm standard error) are the original values without transformation.

Variables	PO1	PO2	PO3	F	P
Individual aboveground fresh weight (g)	5.26 \pm 1.78	4.55 \pm 0.70	4.09 \pm 0.82	0.23	0.80
Individual aboveground dry weight (g)	0.90 \pm 0.19	0.78 \pm 0.09	0.89 \pm 0.16	0.63	0.54
Individual height (cm)	20.84 \pm 4.13	17.86 \pm 1.50	12.12 \pm 3.84	0.21	0.81
Individual leaf area (cm ²)	10.42 \pm 4.67	14.38 \pm 11.79	14.37 \pm 15.61	0.24	0.79

Table A7. Variables measured on *A. hybridus* plants from different seed parents under the four-weed control. PO1, PO2, PO3 represent plants of three seed parents from the organic farm. Mean values (\pm standard error) are the original values without transformation.

Variables	PO1	PO2	PO3	F	P
Individual aboveground fresh weight (g)	37.19 \pm 5.71	38.22 \pm 2.96	34.30 \pm 7.45	0.65	0.56
Individual aboveground dry weight (g)	8.10 \pm 1.17	6.08 \pm 0.8	8.47 \pm 2.51	0.60	0.58
Individual height (cm)	51.47 \pm 5.86	46.29 \pm 3.86	54.92 \pm 7.97	0.50	0.63
Individual leaf area (cm ²)	611.47 \pm 67.31	453.84 \pm 52.41	451.83 \pm 29.83	3.08	0.65

Table A8. Properties of Sunshine Mixed #1 soil. The ingredients of the soil were consisted of Coarse Canadian Sphagnum peat moss, coarse perlite, dolomite and gypsum. Information was provided by the company.

Parameters	Range of value /ppm
pH	5.0 - 5.8
Nitrate Nitrogen	4 - 67
Ammonium Nitrogen	1 - 31
Phosphorus	9 - 42
Potassium	36 - 129
Calcium	37 -158
Magnesium	17 - 77
Sulfur	70 - 225
Manganese	0 - 1.5
Iron	0 - 0.5
Copper	0 - 0.05
Boron	0 - 0.36
Zinc	0 - 0.16
Molybdenum	0 - 0.07

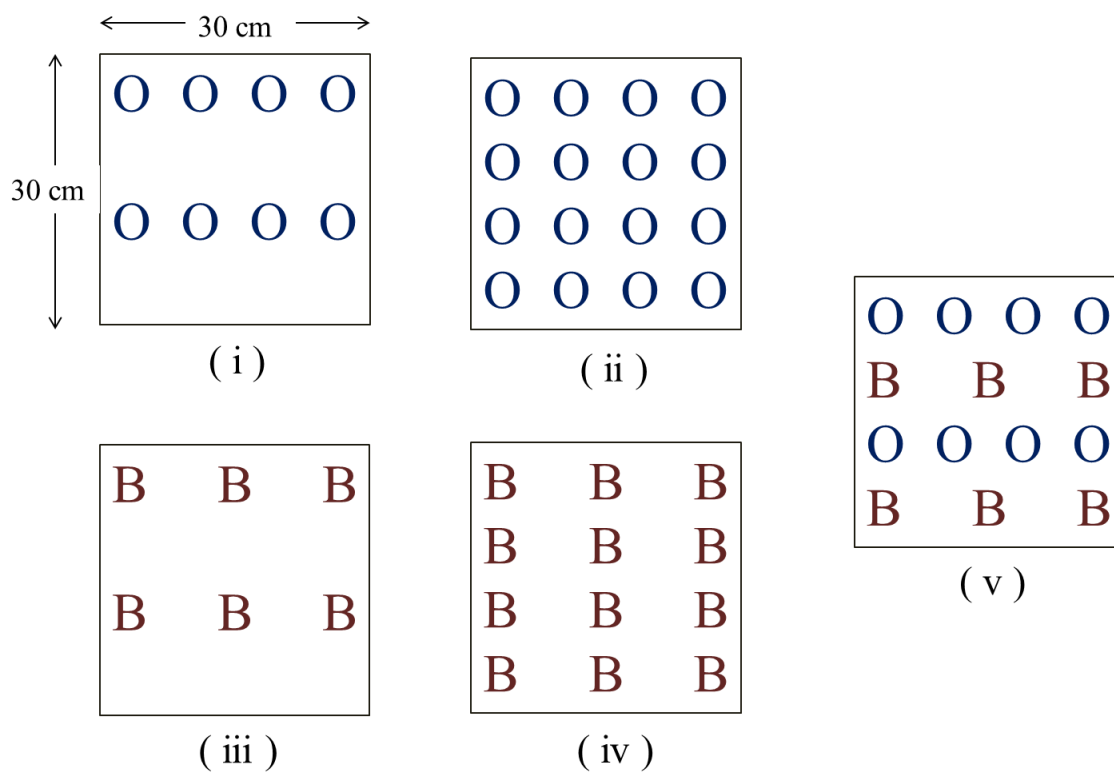


Figure A1. Treatments in Experiment No.1: i) monoculture of eight onions, M8O; ii) monoculture of sixteen onions, M16O; iii) monoculture of six yellow wax beans, M6B; iv) monoculture of twelve yellow wax beans, M12B and v) intercrop of eight onions and six yellow wax beans, IOB.

Table A9. Ingredients of PlantProd All Purpose Fertilizer.

Ingredients	Content
Total Nitrogen	20%
Available Phosphoric Acid / (P ₂ O ₅)	20%
Soluble Potash (K ₂ O)	20%
Boron	0.02%
Chelated Copper (Cu)	0.05%
Chelated Iron (Fe)	0.10%
Chelated Manganese(Mn)	0.05%
Molybdenum (Mo)	0.0005%
Chelated Zinc (Zn)	0.05%
EDTA (Chelating Agent)	1.24%

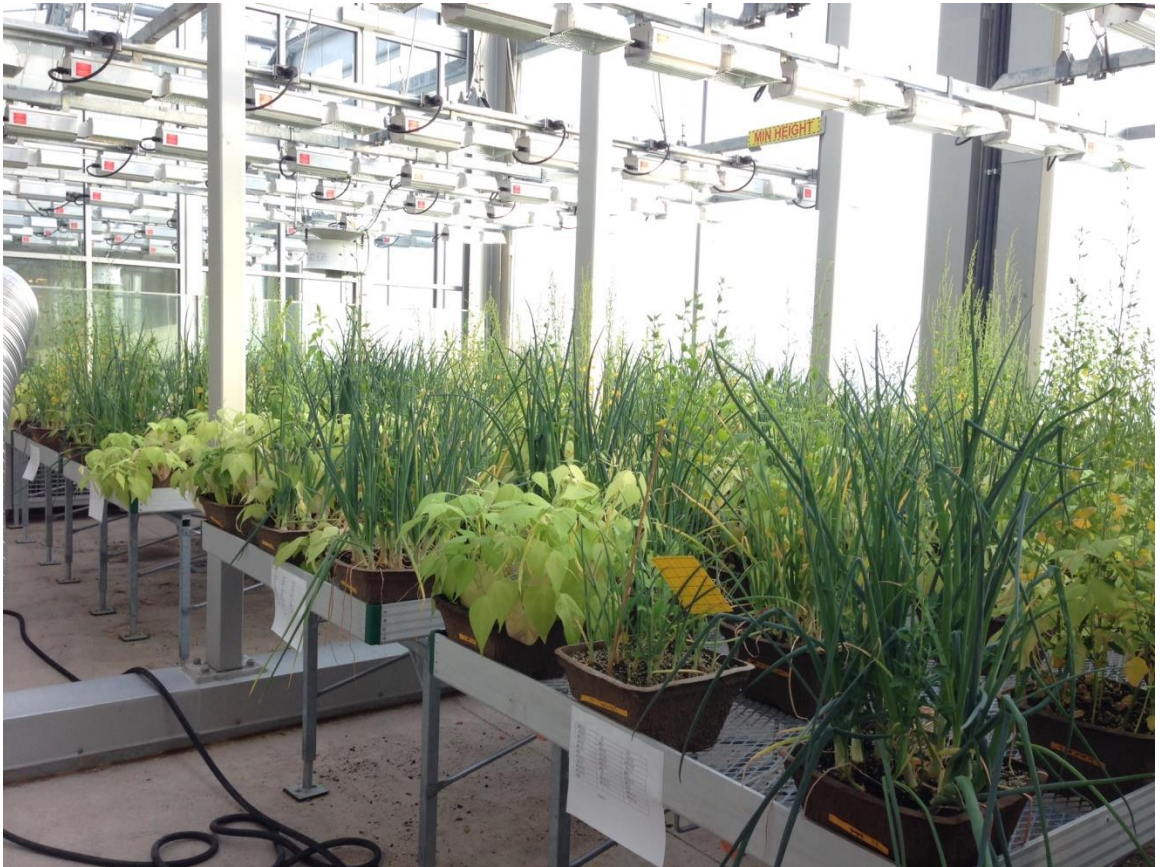


Figure A2. General view of the experiment (4 days before harvest). Greenhouse in Cairns Complex, Brock University (Photo by Yi An Lin).